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Harry J. Bennett (1904-1983)

Gordon Gunter

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**Harry J. Bennett
1904–1983**

Bernice is a small community in Union Parish, Louisiana, a few miles south of the Arkansas line and west of Lake d'Arbon. Harry Jackson Bennett was born there in 1904. He died of a sudden heart stoppage on May 23, 1983, in Baton Rouge, a few weeks short of 79 years of age. He was probably the most telling friend this Laboratory ever had outside of Mississippi.

I met Harry Bennett in 1931 at the Grand Isle marine laboratory of Louisiana State University and we have both tried to promote zoology and the teaching of it ever since. He was a stricter moralist than I, but some of our wants and desires coincided and we cooperated well. When Louisiana State University saw fit to abolish the Grand Isle laboratory it pained us both. We pointed out to the L.S.U. people that this Laboratory was as close as their own had been and that they could join us at little expense. That ploy was successful and in 1956 L.S.U. was the first out-of-state affiliate of the Gulf Coast Research Laboratory. Now there are 57 colleges and universities from South Carolina to Oklahoma to North Dakota formally affiliated with this Laboratory for teaching purposes.

I have heard Bennett say many times that the most important teachers in America were those of the first grade. He took deep interest in all science teaching and promoted it as hard as he could. For many years he taught a course here in the summer, "Marine Zoology for Teachers." The students were mostly women. He got them muddy, made them catch the animals alive, scared them badly, and graded them very gently. They always gave him a party at the end of the session.

After getting a bachelor's degree at L.S.U., Harry Bennett went to the University of Illinois in 1926 as a student of H. B. Ward, who revolutionized parasitology in this country. He took a master's and the doctor's degree there and came back to L.S.U. where he was in the Zoology Department for 45 years. He did stints as Assistant Dean of the College of Arts and Sciences from 1938 to 1942 and director of the Marine Laboratory for ten years (1946–1956). In 1968 he was awarded the Distinguished Faculty Fellowship of the L.S.U. Foundation. He published 32 papers and served as president of the Association of Southeastern Biologists in 1956. He was a member of the American Society of Zoologists, the American Society of Parasitologists, the American Microscopical Society, the Louisiana and Tennessee academies of science, Sigma Xi, Phi Kappa Phi, and the American Malaria Society. He served for several years on the Commission for the Study of Schistosomiasis.

When the last World War came he decided to go and in spite of being color-blind he flimflammed the Army and served in the Sanitary Corps in the Pacific, quite creditably, and came out a Lieutenant Colonel. During his retirement years he performed a task for the Louisiana Academy of Sciences and wrote a fine history of the Academy. It was published in 1983 just before his demise. Harry Bennett always tried and he did very well.

He is survived by his wife, the former Miss Jane Tobie, also of the Ward school, three daughters and six grandchildren.

Gordon Gunter
Ocean Springs, Mississippi
June 24, 1983

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EX-VESSEL VALUE AND SIZE COMPOSITION OF REPORTED MAY–AUGUST CATCHES OF BROWN SHRIMP AND WHITE SHRIMP FROM 1960 TO 1981 AS RELATED TO THE TEXAS CLOSURE¹

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ABSTRACT Indices were used to test for trends in ex-vessel price spread (value per shrimp by size category), size composition, and ex-vessel value composition of the reported May-August catches (inshore and offshore combined) of brown shrimp (*Penaeus aztecus*) and white shrimp (*P. setiferus*) from the Texas coast, the Mississippi River to Texas, and Pensacola to the Mississippi River, from 1960 to 1981. Levels of reported May-August catch and ex-vessel value of the catch also were examined for the same period. Statistical tests were conducted to determine if 1981 was an outlier as compared to other years, in the context of impacts of closure of the fishery conservation zone (FCZ) off Texas to shrimp from May 22 to July 15, 1981, a management measure referred to as the Texas Closure.

INTRODUCTION

The territorial sea of the State of Texas and the adjacent fishery conservation zone (FCZ) were closed to shrimping for brown shrimp (*Penaeus aztecus*) from May 22 to July 15, 1981. This management action was dubbed the Texas Closure by the Gulf of Mexico Fishery Management Council (GMFMC 1980). The territorial sea extends from the coastal baseline to 9 nautical miles off Texas (Figure 1). The FCZ, under federal jurisdiction, extends from the outer limit of Texas' territorial sea to 200 miles from shore. The State of Texas eliminated minimum size restrictions on brown shrimp caught in waters open to shrimping before and after the closure, and allowed daytime fishing for white shrimp to continue in waters up to 4 fm in depth within the territorial sea during the closure. The GMFMC (1980) expected that the Texas Closure would lead to an increase in yield of brown shrimp in the FCZ through additional growth and survival and from abatement of the practice of discarding undersized brown shrimp.

For years, there has been considerable controversy regarding the optimum size at which shrimp should be harvested (GMFMC 1980). During their life cycle, brown shrimp and white shrimp enter inshore waters (landward of barrier islands) as postlarvae, and emigrate a few months later to offshore waters (seaward of barrier islands) as subadults. For that reason, the shrimp caught inshore generally are smaller than those caught offshore. Thus, to a great extent, the size composition of the catch is dependent on where and when the shrimp are caught during each annual cycle. This choice is complicated by the fact that ecological requirements of brown shrimp and white shrimp differ from one another (Christmas and Etzold 1977, GMFMC 1980), and the peaks in abundance of the two species occur out of phase with one

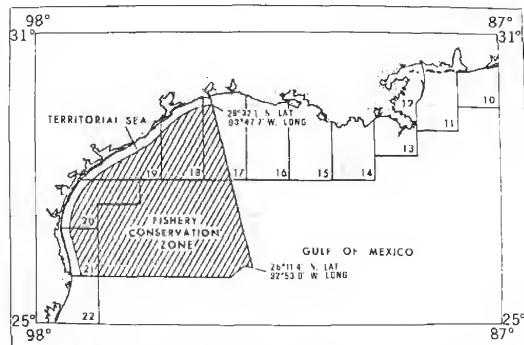


Figure 1. Boundaries of statistical areas 10–21, the Texas territorial sea and the fishery conservation zone off Texas (based on information from GMFMC, 1980).

another. The size at which shrimp are harvested is all the more important, because the ex-vessel price per pound of shrimp increases with their size (Neal 1967, Griffin et al. 1974, Griffin and Nichols 1976, Griffin et al. 1976).

The 1981 Texas Closure provided a unique opportunity for exaggerating the contrast between a management strategy that protects small brown shrimp and allows them to grow to larger sizes before harvest and one that allows small as well as large brown shrimp to be harvested in large quantities. Using yield-per-recruit analysis and a simulation model of shrimp fishing, Nichols (1982) predicted that the brown shrimp yield off Texas in May-August 1981 would be 11.7 million pounds greater than that expected had there been no Texas Closure. Poffenberger (1982) showed that the Texas Closure caused an increase in brown shrimp landings off the Texas coast, which in turn caused a decrease in ex-vessel price per pound. Despite the decrease in price, Poffenberger (1982) concluded that there was an increase in gross revenue by about 21.5 million dollars from the brown

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shrimp fishery in May-August 1981 over what would have been expected had there been no Texas Closure. Klima et al. (1982) stated that recruitment of brown shrimp in Texas bays and size composition of the offshore stock in 1981 were similar to those in previous years of good production. They also stated that the brown shrimp catch per unit effort was higher in 1981 than would have been the case without the Texas Closure. They concluded that the Texas Closure had a positive impact on relative abundance and production of brown shrimp off Texas. Using fishery-independent data, Matthews (1982) reported good catch rates of brown shrimp collected off the coast of Texas during the Texas Closure.

Caillouet and Koi (1981) investigated trends in ex-vessel price spread among shrimp size categories, in size composition, and in ex-vessel value composition of the May-August catches (inshore and offshore combined) of brown shrimp and white shrimp from the Texas, Louisiana, Mississippi, and Alabama coasts, for the years 1960 to 1978. They anticipated use of their analytical approach in assessing future impacts of the Texas Closure. When they chose May-August as the time interval for their analysis, the specific dates for the Texas Closure had not yet been set. They wanted to make sure that the chosen interval would encompass the future closure interval so as to assess immediate impacts of the Texas Closure, including those immediately before and in anticipation of the closure, and those during and immediately after the closure.

While almost half of the May-August period was closed to shrimping for brown shrimp off the Texas coast in 1981, it was open to shrimping in other areas, both inshore and offshore. Caillouet and Koi (1981) based their analyses on inshore and offshore catch data combined. The stocks of shrimp include inshore and offshore components. The possibility that inshore fishing intensity might increase in areas open to shrimping during the Texas Closure (GMFMC 1980), with consequent effects on the combined inshore and offshore catch, provided further justification for combining inshore and offshore catches in the analysis. Furthermore, because the yield from inshore areas represents a significant portion of the total yield, we thought that it should not be ignored in assessing impacts of the Texas Closure. In other words, we did not want to assume that impacts of the Texas Closure were confined only to the offshore fishery.

Two purposes of this paper are to update the analyses of Caillouet and Koi (1981) by adding data from 1979 to 1981, and to compare the observed 1981 indices of ex-vessel price spread, size composition, and ex-vessel value composition of the May-August catches of brown shrimp and white shrimp with those expected for 1981 based on average levels or trends from 1960 to 1981. For the latter purpose, we applied linear trend analyses, employing simple linear regression, to the time series of indices over the years 1960–1981. Our analyses were designed to test the null hypothesis that

the 1981 indices were not significant² "outliers" in the 1960–1981 data series.

Our application of simple linear regression analysis, to detect trends and to test hypotheses concerning indices of ex-vessel price spread, size composition, and ex-vessel value composition of shrimp catches, requires some explanation to guide the reader in interpretation of the results. Simple linear regression analysis tests only for linear trends. If there were strongly curvilinear trends in the indices, linear regression analysis alone would not detect them, and this could also lead to a conclusion that there were no significant (linear) trends. However, inspection of our scatter plots (e.g., Figure 9) of the data points by the reader can be helpful in this regard. When our analysis detected no significant linear trend, a mean index was calculated to represent the time series of points.

As shown in our scatter plots of the indices, two types of 95 percent confidence bands were given. The narrower confidence bands (Figure 9) represented the uncertainty in estimating or predicting the population mean index, depicted by either a regression line or a horizontal line through the data points (for cases where there was no significant linear trend; e.g., Figure 10). The wider confidence bands (Figure 9) represented the uncertainty in estimating or predicting an individual index level for a particular year. In general, 5 percent of the points would be expected to fall outside such confidence bands, due to chance alone. For additional explanation, the reader is referred to Snedecor and Cochran (1967, pp. 153–157).

A third purpose of this paper is to determine whether the three indices were correlated with each other or with the weight of the May-August catches, using the entire time series of indices from 1960 to 1981. We made comparisons among such correlations between species and among coastal areas, in order to distinguish the effects of the Texas Closure from other effects such as year-to-year variations in recruitment, fishing effort, or both.

METHODS

Description of data

Summations of the May-August catches (inshore and offshore combined) for brown shrimp and white shrimp and their ex-vessel value were compiled from data files available from the National Marine Fisheries Service (NMFS), Southeast Fisheries Center (SEFC), Technical and Information Management Services (TIMS). The data for 1979, 1980, and 1981 were those available from the TIMS in February 1982. The reader is cautioned that the 1980 and 1981 data may have undergone slight changes by the TIMS since then, based upon identification of minor errors and upon minor additions

²Refers throughout this paper to the 95% level of confidence.

to the data files. Historically, such updating of the files has not been of major consequence.

The characteristics of shrimp catch data were described previously (Caillouet and Koi 1981). Data for 1960 to 1978 were obtained from Caillouet and Koi (1981). The weight of the reported May-August catches (inshore and offshore combined) was expressed in pounds (heads off) and the ex-vessel value in dollars (unadjusted for effects of inflation) for each year, coastal area, species, and size category (< 15, 15–20, 21–25, 26–30, 31–40, 41–50, 51–67, and ≥ 68 count), and "pieces," representing parts of shrimp tails that could not be assigned to a size category.

Separate analyses were conducted for both species and three coastal areas (Figure 1), which were distinguished as follows: 1) Texas coast (statistical areas 18–21 combined); 2) Mississippi River to Texas (statistical areas 13–17 combined), representing that part of the Louisiana coast west of the Mississippi River; and 3) Pensacola to the Mississippi River (statistical areas 10–12 combined), representing that part of the Louisiana coast east of the Mississippi River, the Mississippi coast, the Alabama coast, and a small part of the upper west coast of Florida (catches from Pensacola Bay are excluded from this area, as they are allocated to the adjacent Apalachicola area by the TIMS). Note that almost half of statistical area 17 was included in the area that was closed to shrimping from May 22 to July 15, 1981 (Figure 1). Therefore, for the years 1960 to 1980, the May-August catch statistics for the Mississippi River to Texas coastal area represent a somewhat larger zone open to shrimping than was the case in 1981, as a result of the Texas Closure.

ANALYTICAL RESULTS

The analytical methods followed those of Caillouet and Koi (1981).

May-August catches

Table 1 provides background concerning both the magnitude and stability of the percentage of the May-August catch (all size categories as well as "pieces" combined) taken inshore vs. offshore, for each species and coastal area from 1960 to 1981. For brown shrimp, the percentage of the May-August catch taken inshore was lowest for the Texas coast (10%), intermediate for Pensacola to the Mississippi River (50%), and highest for the Mississippi River to Texas (54%). This elucidates the emphasis on offshore fishing in Texas and on both inshore and offshore fishing in the other two coastal areas. However, the inshore proportion of the May-August brown shrimp catch has been increasing on the Texas coast and in the Pensacola to the Mississippi River area, while it has been decreasing in the Mississippi River to Texas area. For white shrimp, the percentage of the May-August catch taken inshore was highest for Pensacola to the Mississippi River (62%), intermediate for the Texas coast (54%), and lowest for the Mississippi River to Texas (32%). This percentage showed no significant trend for the Texas coast and Mississippi River to Texas, but there was a significant downward

TABLE I.
Percentages of the May-August catches (inshore and offshore combined) of brown shrimp and white shrimp taken inshore, and percentages of the calendar year annual catches (inshore and offshore combined) of brown shrimp and white shrimp taken during May-August, for the Texas Coast, the Mississippi River to Texas, and Pensacola to the Mississippi River, during 1960 to 1981.

Species	Coastal Area	Percentage May-August Catch Taken Inshore		Percentage Annual Catch Taken in May-August	
		Mean ^a	Range	Mean ^a	Range
Brown Shrimp	Texas Coast	10 ^b	0 ^c –29	58	47–73
	Mississippi River to Texas	54 ^d	35–68	81	74–90
	Pensacola to Mississippi River	50 ^e	34–76	84	75–93
White Shrimp	Texas Coast	54	30–78	24	16–34
	Mississippi River to Texas	32	11–47	19	8–25
	Pensacola to Mississippi River	62 ^f	29–94	13	5–23

^a Averaged over all years from 1960 to 1981.

^b There was a significant upward trend in percentage from 1960 to 1981: $Y = -46.2 + 0.8X$, where Y = percentage, and X = last two digits (60–81) of each year (1960–1981). The coefficient of determination, r^2 , was 0.55.

^c Rounded to zero, but the percentage was 0.04.

^d There was a significant downward trend in percentage from 1960 to 1981: $Y = 109.0 - 0.8X$. See footnote b for definitions of Y and X . The coefficient of determination, r^2 , was 0.26.

^e There was a significant downward trend in percentage from 1960 to 1981: $Y = -41.6 + 1.3X$. See footnote b for definitions of Y and X . The coefficient of determination, r^2 , was 0.61.

^f There was a significant downward trend in percentage from 1960 to 1981: $Y = 206.2 - 2.0X$. See footnote b for definitions of Y and X . The coefficient of determination, r^2 , was 0.50.

trend in this percentage for Pensacola to the Mississippi River.

The percentage of the calendar year annual catch of brown shrimp represented by the May-August catch of brown shrimp is shown in Table 1, for each coastal area. Likewise, a similarly calculated percentage is shown for white shrimp. There were no significant trends in this percentage for either species in any of the three coastal areas from 1960 to 1981. For Pensacola to the Mississippi River, the May-August brown shrimp catch represented 84% of the annual catch, on the average. For the Mississippi River to Texas it averaged 58%, and for the Texas coast 54%. Thus, a substantial percentage of the annual brown shrimp catch was taken in May-August within each coastal area. The lower percentage for the Texas coast reflects the emphasis on offshore fishing with its consequent protracted harvest. For

white shrimp, the average percentage of the annual catch taken in May-August was highest for the Texas coast (24%), intermediate for the Mississippi River to Texas (19%), and lowest for Pensacola to the Mississippi River (13%). These low percentages reflected the later harvest of white shrimp, compared to brown shrimp, determined by differences in phasing of life cycle events in these two species.

Within each coastal area, the May-August catch of brown shrimp greatly exceeded that of white shrimp in all years from 1960 to 1981 (Figures 2-7). In all years, the May-August brown shrimp catches from the Mississippi River to

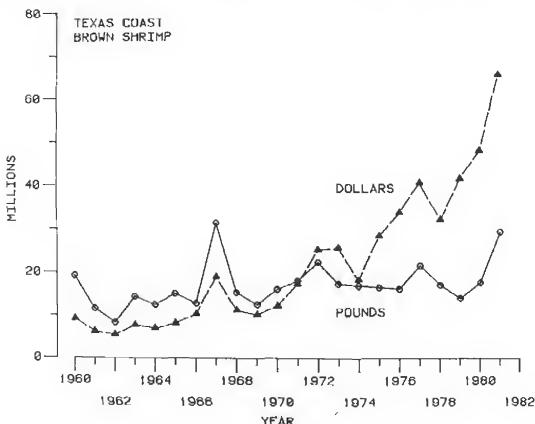


Figure 2. Weight (millions of pounds, heads off) and ex-vessel value (millions of dollars) of reported May-August catches (inshore and offshore combined) of brown shrimp from the Texas coast (statistical areas 18-21 combined), 1960-1981.

Texas exceeded those from Pensacola to the Mississippi River, and in most years, including 1981, they exceeded those from the Texas coast. The May-August catch of brown shrimp from the Texas coast was higher in 1981 than in any previous year except 1967, and the ex-vessel value of this catch was at an unprecedented high for the Texas coast (Figure 2). The May-August brown shrimp catches from the other two coastal areas in 1981 were higher than in 1980, but did not exceed those of all previous years in the 1960-1980 series (Figures 4 and 6).

Despite the fact that the May-August brown shrimp catch from the Texas coast (29.6 million lb., Figure 2) in 1981 was lower than that from the Mississippi River to Texas (38.4 million lb., Figure 4), it had a greater ex-vessel value (66.3 million dollars) than that from the Mississippi River to Texas (56.8 million dollars). In 1981, the ex-vessel value (19.3 million dollars) of the May-August brown shrimp catch from Pensacola to the Mississippi River (10.4 million lb.) was much lower than for the other two areas, as was the case in all previous years.

The May-August catch of white shrimp from the Texas coast (1.7 million lb., Figure 3) in 1981 was lower than that

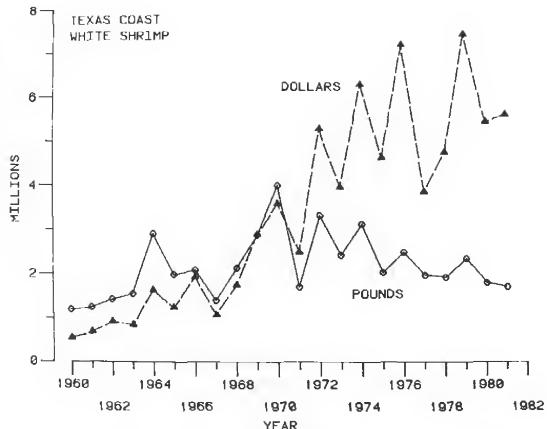


Figure 3. Weight (millions of pounds, heads off) and ex-vessel value (millions of dollars) of reported May-August catches (inshore and offshore combined) of white shrimp from the Texas coast (statistical areas 18-21 combined), 1960-1981.

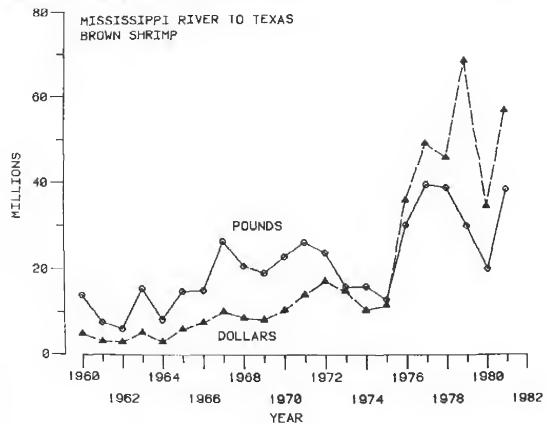


Figure 4. Weight (millions of pounds, heads off) and ex-vessel value (millions of dollars) of reported May-August catches (inshore and offshore combined) of brown shrimp from the Mississippi River to Texas (statistical areas 13-17 combined), 1960-1981.

from the Mississippi River to Texas (7.8 million lb., Figure 5), and the ex-vessel value of this catch (5.6 million dollars) was dramatically lower than that from the Mississippi River to Texas (26.6 million dollars). The May-August white shrimp catches from the Mississippi River to Texas and from Pensacola to the Mississippi River in 1981 were somewhat higher than in 1980, but the opposite was true for the Texas coast. In all years, the May-August white shrimp catch from the Mississippi River to Texas exceeded that from the Texas coast, and both exceeded that from Pensacola to the Mississippi River. The ex-vessel value of the May-August catch of white shrimp from the Mississippi River to Texas in 1981 was at an all time high. While the ex-vessel value of the

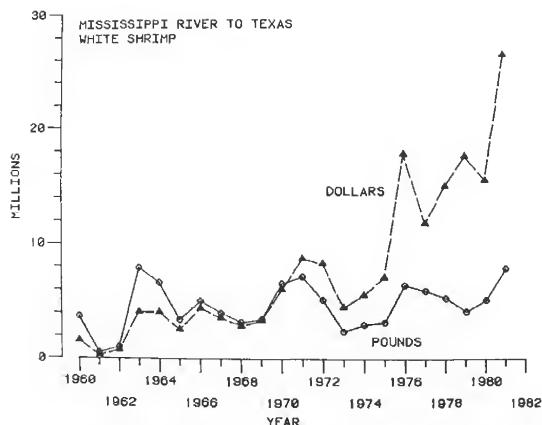


Figure 5. Weight (millions of pounds, heads off) and ex-vessel value (millions of dollars of reported May-August catches (inshore and offshore combined) of white shrimp from the Mississippi River to Texas (statistical areas 13–17 combined), 1960–1981.

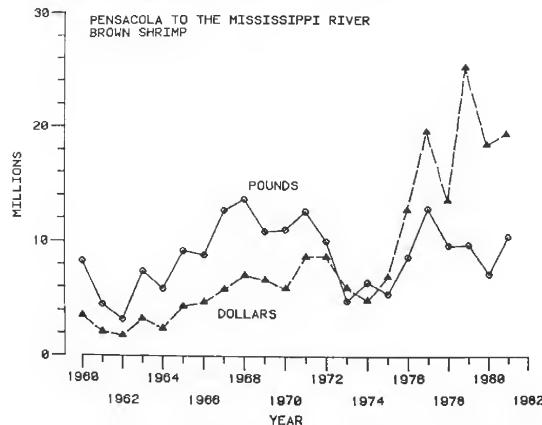


Figure 6. Weight (millions of pounds, heads off) and ex-vessel value (millions of dollars) of reported May-August catches (inshore and offshore combined) of brown shrimp from Pensacola to the Mississippi River (statistical areas 10–12 combined), 1960–1981.

May-August catch of white shrimp from Pensacola to the Mississippi River in 1981 was higher than that in most years in the 1960–1980 series, it did not exceed that in 1977 and 1979.

May-August ex-vessel value per shrimp by size category

Caillouet and Koi (1981) used the logarithmic form of the following model to estimate parameters a and b by linear regression, for each species, coastal area, and year from 1960 to 1978, and we updated this series through 1981 (Tables 2–4):

$$\hat{V}_i = a (\exp b C_i) \quad (1)$$

where V_i = May-August average ex-vessel value (dollars per

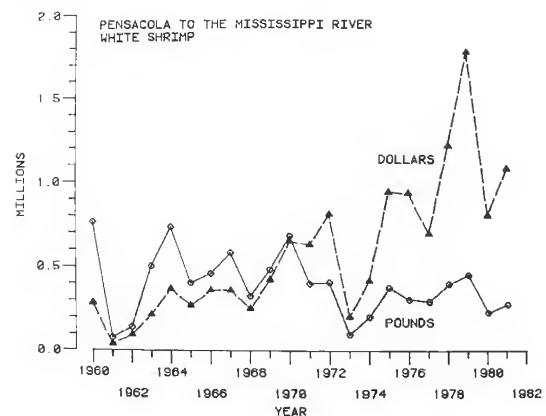


Figure 7. Weight (millions of pounds, heads off) and ex-vessel value (millions of dollars) of reported May-August catches (inshore and offshore combined) of white shrimp from Pensacola to the Mississippi River (statistical areas 10–12 combined), 1960–1981.

shrimp) for the i th size category, C_i = lower limit (count) of the i th size category ($C_1 = 15$, $C_2 = 21$, $C_3 = 26$, $C_4 = 31$, $C_5 = 41$, $C_6 = 51$, and $C_7 = 68$), and $i = 1, 2, \dots, 7$. An example of the relationship between V and C is shown in Figure 8A, based on the May-August brown shrimp catch from the Texas coast in 1981. An example of the fitted logarithmic form of model 1 is given in Figure 8B. The very high coefficients of determination, r^2 , for the logarithmic form of model 1 indicated that straight lines fitted the data for each year very well (Tables 2–4, see also Caillouet and Koi 1981). All slopes, b , of the straight lines were negative, showing that the ex-vessel price per shrimp decreased logarithmically with increase in count (decrease in size). The slope, b , of each straight line is a simple index of the May-August ex-vessel price spread among the size categories of shrimp in any given year.

TABLE 2.
Parameter estimates^a of linear regressions of transformed ex-vessel price (dollars per shrimp), $\ln V$, on count, C , for reported May-August catches (inshore and offshore combined) of brown shrimp and white shrimp from the Texas coast (statistical areas 18–21 combined), 1979–1981.

Year	Brown Shrimp ^b			White Shrimp ^b		
	a	b	r^2	a	b	r^2
1979	0.80614	-0.05504	0.996	0.70034	-0.05206	0.979
1980	0.59210	-0.05101	0.994	0.49137	-0.04706	0.985
1981	0.51354	-0.05318	0.966	0.60401	-0.05432	0.948

^a $\ln(a) = \text{intercept}$, $b = \text{slope}$, and $r^2 = \text{coefficient of determination}$.

^b Results of similar analyses of data from 1960 to 1978 can be found in Caillouet and Koi (1981).

TABLE 3.

Parameter estimates^a of linear regressions of transformed ex-vessel price (dollars per shrimp), $\ln V$, on count, C, for reported May-August catches (inshore and offshore combined) of brown shrimp and white shrimp from the Mississippi River to Texas (statistical areas 13-17 combined), 1979-1981.

Year	Brown Shrimp ^b			White Shrimp ^b		
	a	b	r^2	a	b	r^2
1979	0.77312	-0.05398	0.995	0.81161	-0.05504	0.990
1980	0.56006	-0.05004	0.995	0.56161	-0.05018	0.992
1981	0.57987	-0.05529	0.976	0.73555	0.05975	0.976

^a $\ln(a)$ = intercept, b = slope, and r^2 = coefficient of determination.

^b Results of similar analyses of data from 1960 to 1978 can be found in Caillouet and Koi (1981).

TABLE 4.

Parameter estimates^a of linear regressions of transformed ex-vessel value (dollars per shrimp), $\ln V$, on count, C, for reported May-August catches (inshore and offshore combined) of brown shrimp and white shrimp from Pensacola to the Mississippi River (statistical areas 10-12 combined), 1979-1981.

Year	Brown Shrimp ^b			White Shrimp ^b		
	a	b	r^2	a	b	r^2
1979	0.73353	-0.05047	0.989	0.73061	-0.05045	0.980
1980	0.53505	-0.04767	0.987	0.52388	-0.04739	0.985
1981	0.56535	-0.05258	0.972	0.62225	-0.05482	0.944

^a $\ln(a)$ = intercept, b = slope, and r^2 = coefficient of determination.

^b Results of similar analyses of data from 1960 to 1978 can be found in Caillouet and Koi (1981).

We excluded the < 15 size category from model 1 so as to be consistent with previous work, and because the line representing the logarithmic form of model 1 is not straight in the region of < 15 count (Caillouet and Koi 1981). The < 15 category represented $\leq 3\%$ of the weight of the May-August catches of brown shrimp in any of the three coastal areas in any given year. In 1981, the < 15 category represented 0.2% of the May-August catches of brown shrimp from the Texas coast, 0.2% from the Mississippi River to Texas, and 0.1% from Pensacola to the Mississippi River. In any given year, the < 15 category represented as high as 23% of the May-August white shrimp catches from the Texas coast (15.6% in 1981), 15% from the Mississippi River to Texas (5.1% in 1981), and 28% from Pensacola to the Mississippi River (3.6% in 1981). The category "pieces" also was excluded from model 1, because it represents parts of shrimp tails which could not be assigned to a size category.

To determine whether there were significant trends in the index of ex-vessel price spread among size categories, we calculated the linear regression of b on the last two digits

(60-81) of each year from 1960 to 1981, for both species and all three coastal areas (Table 5). There were significant downward trends in b for brown shrimp in all three coastal areas (Figures 9, 11, and 13) and for white shrimp from the Mississippi River to Texas (Figure 12) and Pensacola to the Mississippi River (Figure 14), but there was no significant trend in b for white shrimp from the Texas coast (Figure 10).

The downward trends indicated that the May-August ex-vessel price spread among size categories increased during the period from 1960 to 1981. Because there was no significant trend in b for white shrimp from the Texas coast, we calculated the mean of the indices for the years 1960-1981 and plotted the mean as a horizontal solid line through the points in Figure 10. No data point for 1972 was included in calculating the regression trend for white shrimp from Pensacola to the Mississippi River, because no catch was reported for the ≥ 68 count category in 1972 (Caillouet and Koi 1981).

Within each coastal area, the ex-vessel price spread index b for brown shrimp in May-August 1981 fell within the 95% confidence bands for individual levels of b (Figures 9, 11, and 13), indicating that there was no significant departure in 1981 from the expected increase in ex-vessel price spread

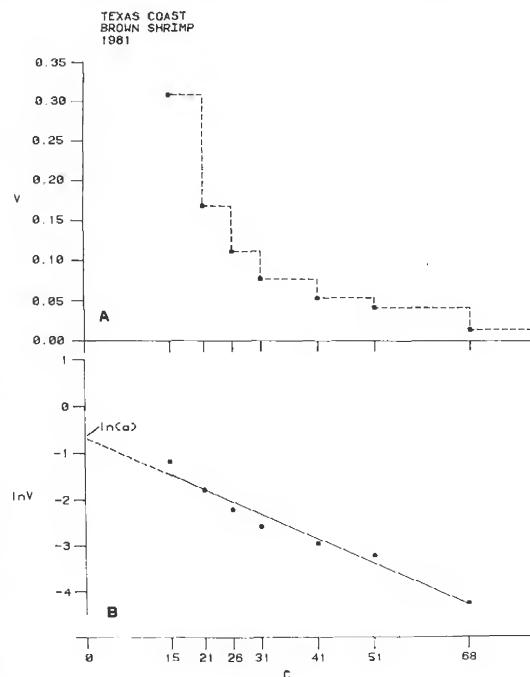


Figure 8. Relationship between the ex-vessel price (dollars per shrimp), V, and count, C, for the reported May-August catch (inshore and offshore combined) of brown shrimp from the Texas coast (statistical areas 18-21 combined) in 1982 (graph A). In graph B, the line was fitted by linear regression (see Table 2).

TABLE 5.

Results of tests for trends^a in ex-vessel price spread index b, in size composition index d, and in ex-vessel value composition index h, for reported May-August catches (inshore and offshore combined) of brown shrimp and white shrimp from the Texas coast, the Mississippi River to Texas, and Pensacola to the Mississippi River, during 1960 to 1981
(indices b, d and h are defined in the text).

Species	Coastal Area		For Ex-vessel Price Spread Index b	For Size Composition Index d	For Ex-vessel Value Composition Index h
Brown Shrimp	Texas Coast	Trend ^a	-0.0003 ^b	0.0024 ^b	0.0023 ^b
		Intercept	-0.0332	-0.2183	-0.2353
		Trend Coefficient of Determination	0.222	0.641	0.624
	Mississippi River to Texas	Sum of Squares ^c	0.000290	0.002776	0.002932
		Trend	-0.0005 ^b	0.0003 ^b	0.0002
		Intercept	-0.0187	-0.0273	-0.0281
Brown Shrimp	Pensacola to Mississippi River	Trend Coefficient of Determination	0.367	0.334	0.065
		Sum of Squares	0.000376	0.000120	0.000317
		Trend	-0.0006 ^b	0.0008 ^b	0.0006 ^b
	Texas Coast	Intercept	-0.0091	-0.0798	-0.0711
		Trend Coefficient of Determination	0.486	0.396	0.221
		Sum of Squares	0.000319	0.000904	0.001067
White Shrimp	Mississippi River to Texas	Trend	-0.0002	0.0007	0.0007
		Intercept	-0.0349	-0.1015	-0.1137
		Trend Coefficient of Determination	0.092	0.061	0.035
	Pensacola to Mississippi River	Sum of Squares	0.000499	0.007437	0.011162
		Trend	-0.0006 ^b	0.0009 ^b	0.0004
		Intercept	-0.0124	-0.1076	-0.0879
White Shrimp	Texas Coast	Trend Coefficient of Determination	0.361	0.215	0.043
		Sum of Squares	0.000488	0.002834	0.003594
		Trend	-0.0005 ^b	-0.0003	-0.0009
	Mississippi River to Texas	Intercept	-0.0143	-0.0163	0.0144
		Trend Coefficient of Determination	0.296	0.025	0.168
		Sum of Squares	0.000514	0.002274	0.003297

^a For each species and coastal area, the trends are represented by the slopes of the linear regressions of indices b, d, and h, respectively, on X, where X represents the last two digits (60–81) of each year, 1960–1981. The indices b, d, and h are shown in Tables 2–4, 6–8, and 9–11, respectively, for the years 1979–1981, and in Caillouet and Koi (1981) for the years 1960–1978. Data for 1972 were excluded from regressions for white shrimp from Pensacola to the Mississippi River (see Caillouet and Koi 1981).

^b Trend (slope) was significantly different from zero at the 95% level of confidence.

^c Sum of squares of deviations from linear regression.

for brown shrimp in any of the three coastal areas. The same was true for the May-August 1981 ex-vessel price spread index for white shrimp from the Mississippi River to Texas and from Pensacola to the Mississippi River (Figures 12 and 14). The May-August 1981 ex-vessel price spread index for white shrimp from the Texas coast fell within the 95% confidence limits for individual levels of b (Figure 10), indicating that there was no significant departure in 1981 from the expected price spread based on the mean price spread index. Thus, based upon the inherent variations and trends in ex-vessel price spread, the May-August price spread

index was not a significant outlier in the 1960–1981 time series.

May-August cumulative catch by size category

Caillouet and Koi (1981) used the logarithmic form of the following model to estimate parameters c and d by linear regression for each species, coastal area, and year from 1960 to 1978, and we updated this through 1981 (Tables 6–8):

$$\hat{P}_i = c(\exp dC_i) \quad (2)$$

where P_i = cumulative weight (pounds, heads off) of the

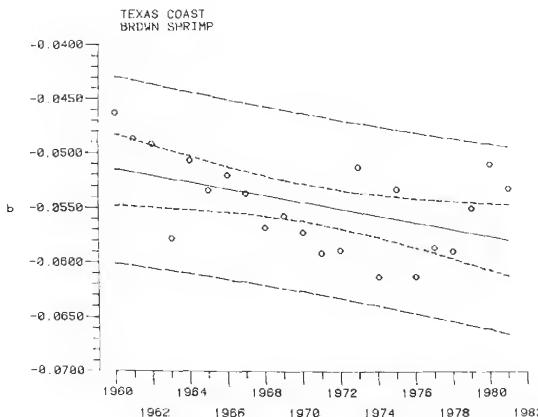


Figure 9. Trend (solid line) in the ex-vessel price spread index b (open circles) for reported May-August catches (inshore and offshore combined) of brown shrimp from the Texas coast (statistical areas 18–21 combined), 1960–1981 (data from Tables 2 and 5, and Caillouet and Koi 1981). The 95% confidence bands are shown for the trend line by short dashes and for individual values of b by long dashes.

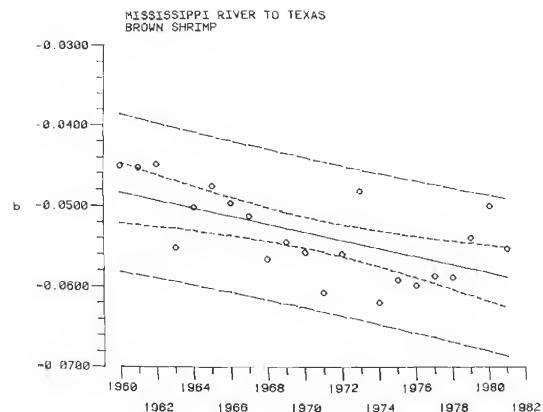


Figure 11. Trend (solid line) in the ex-vessel price spread index b (open circles) for reported May-August catches (inshore and offshore combined) of brown shrimp from the Mississippi River to Texas (statistical areas 13–17 combined), 1960–1981 (data from Tables 3 and 5, and Caillouet and Koi 1981). The 95% confidence bands are shown for the trend line by short dashes and for individual values of b by long dashes.

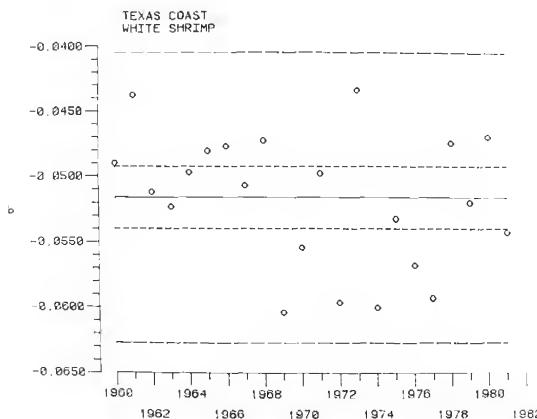


Figure 10. Mean (solid line) ex-vessel price spread index b (open circles) for reported May-August catches (inshore and offshore combined) of white shrimp from the Texas coast (statistical areas 18–21 combined), 1960–1981 (data from Table 2, and Caillouet and Koi 1981). The 95% confidence limits are shown for the mean by short dashes and for individual values of b by long dashes.

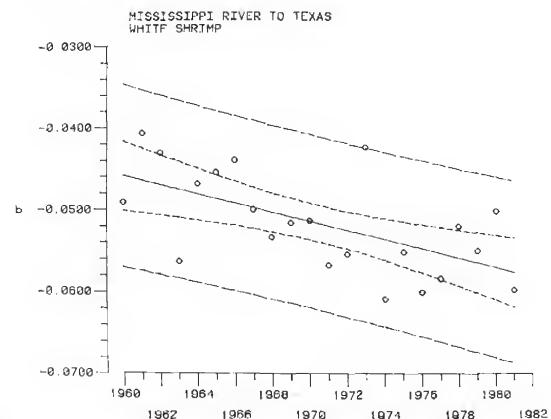


Figure 12. Trend (solid line) in the ex-vessel price spread index b (open circles) for reported May-August catches (inshore and offshore combined) of white shrimp from the Mississippi River to Texas (statistical areas 13–17 combined), 1960–1981 (data from Tables 3 and 5, and Caillouet and Koi 1981). The 95% confidence bands are shown for the trend line by short dashes and for individual values of b by long dashes.

May-August catch in the i th size category. The catches in each size category were cumulated starting with the size category of smallest shrimp (highest count, ≥ 68) and continuing toward the size category of largest shrimp (lowest count, 15–20). An example of the relationship between P and C is shown in Figure 15A, for brown shrimp from the Texas coast in 1981. An example of the fitted logarithmic form of model 2 is shown in Figure 15B. The coefficients of determination for the straight lines representing each year

were very high (Tables 6–8, see also Caillouet and Koi 1981). All slopes, d , were negative, which reflected the construction of model 2 by cumulating catches from small-shrimp to large-shrimp size categories (Caillouet and Koi 1981). The slope, d , of each straight line is a simple index of the size composition of the May-August catch in any given year.

In each year, the levels of d for brown shrimp were lowest for the Texas coast, intermediate for Pensacola to

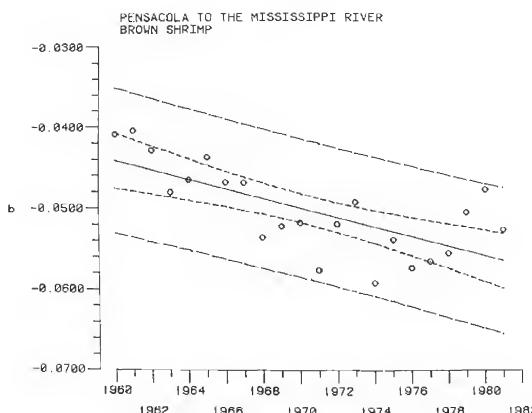


Figure 13. Trend (solid line) in the ex-vessel price spread index b (open circles) for reported May-August catches (inshore and offshore combined) of brown shrimp from Pensacola to the Mississippi River (statistical areas 10–12 combined), 1960–1981 (data from Tables 4 and 5, and Caillouet and Koi 1981). The 95% confidence bands are shown for the trend line by short dashes and for individual values of b by long dashes.

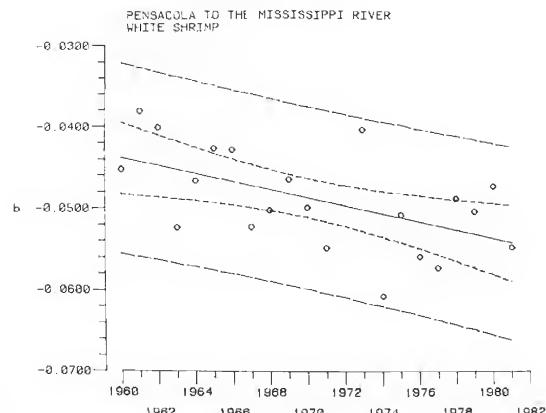


Figure 14. Trend (solid line) in the ex-vessel price spread index b (open circles) for reported May-August catches (inshore and offshore combined) of white shrimp from Pensacola to the Mississippi River (statistical areas 10–12 combined), 1960–1981 (data from Tables 4 and 5, and Caillouet and Koi 1981). The 95% confidence bands are shown for the trend line by short dashes and for individual values of b by long dashes.

TABLE 6.

Parameter estimates^a of linear regressions of transformed cumulative weight (pounds, heads off) of catch, $\ln P$, on count, C , for reported May-August catches (inshore and offshore combined) of brown shrimp and white shrimp from the Texas coast (statistical areas 18–21 combined), 1979–1981.

Year	Brown Shrimp ^b			White Shrimp ^b		
	c	d	r^2	c	d	r^2
1979	20,674,053	-0.02112	0.973	3,332,356	-0.02300	0.890
1980	30,730,002	-0.02805	0.966	3,766,437	-0.04225	0.960
1981	62,640,964	-0.03768	0.962	2,577,937	-0.03633	0.983

^a $\ln(c)$ = intercept, d = slope, and r^2 = coefficient of determination.

^b Results of similar analyses of data from 1960 to 1978 can be found in Caillouet and Koi (1981).

the Mississippi River, and highest for the Mississippi River to Texas (Tables 6–8; Figures 16, 18, and 20; see also Caillouet and Koi 1981). This indicated that the brown shrimp in the May-August catches from the Texas coast were consistently larger than those from Pensacola to the Mississippi River, and those from Pensacola to the Mississippi River were consistently larger than those from the Mississippi River to Texas. No such obvious differences in size of white shrimp in the May-August catches were apparent among the three coastal areas (Figures 17, 19, and 21).

To determine if there were significant trends in the index of size composition of the May-August catches, we calculated the linear regression of d on the last two digits (60–81) of each year, from 1960 to 1981, for both species and for each of the three coastal areas (Table 5). There were

TABLE 7.

Parameter estimates^a of linear regressions of transformed cumulative weight (pounds, heads off) of catch, $\ln P$, on count, C , for reported May-August catches (inshore and offshore combined) of brown shrimp and white shrimp from the Mississippi River to Texas (statistical areas 13–17 combined), 1979–1981.

Year	Brown Shrimp ^b			White Shrimp ^b		
	c	d	r^2	c	d	r^2
1979	35,340,494	-0.00930	0.975	8,456,112	-0.04473	0.994
1980	21,930,962	-0.00516	0.962	6,638,058	-0.02483	0.977
1981	45,344,072	-0.00834	0.971	10,709,053	-0.03012	0.979

^a $\ln(c)$ = intercept, d = slope, and r^2 = coefficient of determination.

^b Results of similar analyses of data from 1960 to 1978 can be found in Caillouet and Koi (1981).

significant upward trends in d for brown shrimp in all three coastal areas (Figures 16, 18, and 20), and for white shrimp from the Mississippi River to Texas (Figure 19), but there were no significant trends in d for white shrimp from the Texas coast (Figure 17) or for white shrimp from Pensacola to the Mississippi River (Figure 21). The significant upward trends for brown shrimp indicated that the size of brown shrimp in the reported May-August catches generally decreased in all three coastal areas from 1960 to 1981. The same was true for May-August white shrimp catches from the Mississippi River to Texas. The absence of significant trends in d for white shrimp catches from the Texas coast and from Pensacola to the Mississippi River indicated that there were no significant trends in size composition of the May-August catches in these two coastal areas. In these two

TABLE 8.

Parameter estimates^a of linear regressions of transformed cumulative weight (pounds, heads off) of catch, $\ln P$, on count, C, for reported May-August catches (inshore and offshore combined) of brown shrimp and white shrimp from Pensacola to the Mississippi River (statistical areas 10-12 combined), 1979-1981.

Year	Brown Shrimp ^b			White Shrimp ^b		
	c	d	r^2	c	d	r^2
1979	13,586,810	-0.01427	0.849	707,215	-0.03047	0.936
1980	11,481,757	-0.02219	0.956	224,118	0.02600	0.926
1981	14,635,344	-0.01490	0.879	369,793	-0.03877	0.969

^a $\ln(c)$ = intercept, d = slope, and r^2 = coefficient of determination.

^b Results of similar analyses of data from 1960 to 1978 can be found in Caillouet and Koi (1981).

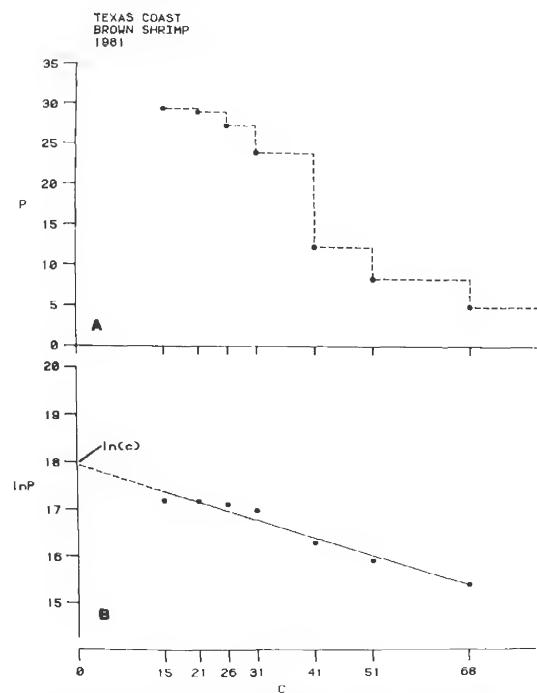


Figure 15. Relationship between the cumulative weight (millions of pounds, heads off) of catch, P, and count, C, for the reported May-August catch (inshore and offshore combined) of brown shrimp from the Texas coast (statistical areas 18-21 combined) in 1981 (graph A). In graph B, the line was fitted by linear regression (see Table 6).

cases, the mean of the indices from 1960 to 1981 was calculated as a horizontal line through the points (Figures 17 and 21). The data point for 1972 was excluded from calculation of the mean index for white shrimp from Pensacola to the Mississippi River (Figure 21), as in the previous section con-

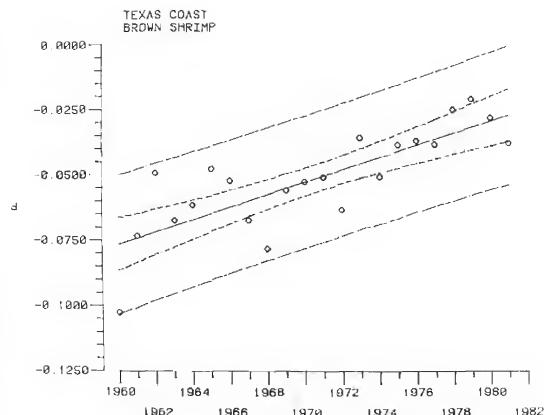


Figure 16. Trend (solid line) in the size composition index d (open circles) for reported May-August catches (inshore and offshore combined) of brown shrimp from the Texas coast (statistical areas 18-21 combined), 1960-1981 (data from Tables 5 and 6, and Caillouet and Koi 1981). The 95% confidence bands are shown for the trend line by short dashes and for individual values of d by long dashes.

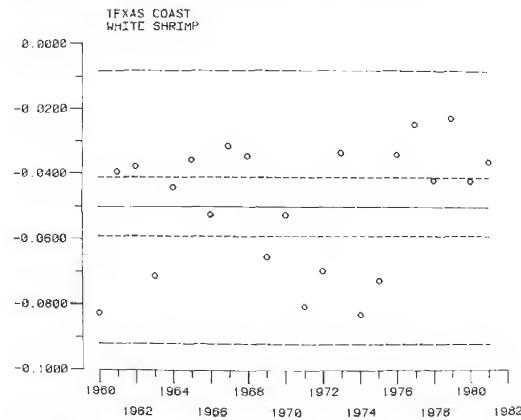


Figure 17. Mean (solid line) size composition index d (open circles) for reported May-August catches (inshore and offshore combined) of white shrimp from the Texas coast (statistical areas 18-21 combined), 1960-1981 (data from Table 6, and Caillouet and Koi 1981). The 95% confidence limits are shown for the mean by short dashes and for individual values of d by long dashes.

cerning the trend in price spread for white shrimp from this coastal area.

Within each coastal area, the size composition index d for brown shrimp catches in May-August 1981 fell within the 95% confidence bands for individual levels of d (Figures 16, 18, and 20), indicating that there was no significant departure in 1981 from the trend of decrease in size. In fact, though the size composition index for 1981 fell outside the 95% confidence interval for the trend lines (Figures 16, 18, and 20), it barely did so, emphasizing its closeness to the

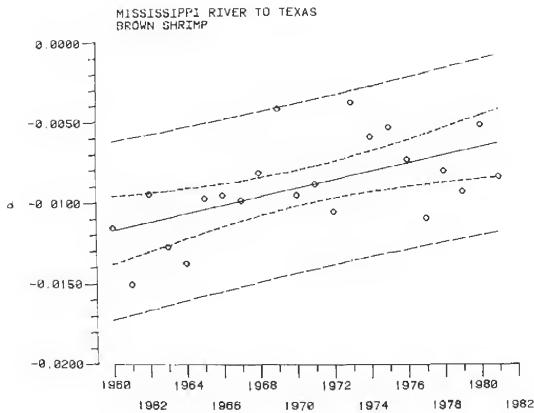


Figure 18. Trend (solid line) in the size composition index d (open circles) for reported May-August catches (inshore and offshore combined) of brown shrimp from the Mississippi River to Texas (statistical areas 13–17 combined), 1960–1981 (data from Tables 5 and 7, and Caillouet and Koi 1981). The 95% confidence bands are shown for the trend line by short dashes and for individual values of d by long dashes.

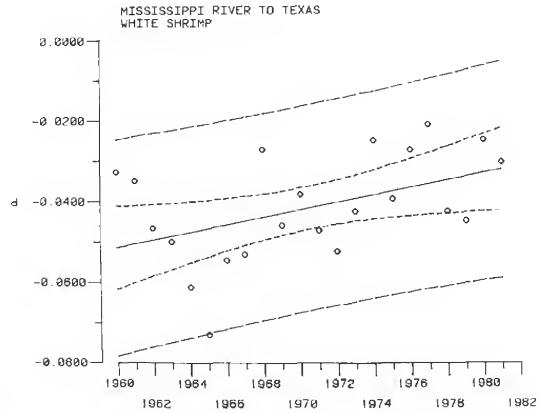


Figure 19. Trend (solid line) in the size composition index d (open circles) for reported May-August catches (inshore and offshore combined) of white shrimp from the Mississippi River to Texas (statistical areas 13–17 combined), 1960–1981 (data from Tables 5 and 7, and Caillouet and Koi 1981). The 95% confidence bands are shown for the trend line by short dashes and for individual values of d by long dashes.

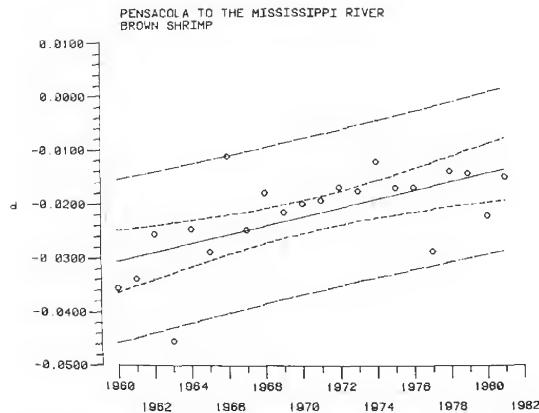


Figure 20. Trend (solid line) in the size composition index d (open circles) for reported May-August catches (inshore and offshore combined) of brown shrimp from Pensacola to the Mississippi River (statistical areas 10–12 combined), 1960–1981 (data from Tables 5 and 8, and Caillouet and Koi 1981). The 95% confidence bands are shown for the trend line by short dashes and for individual values of d by long dashes.

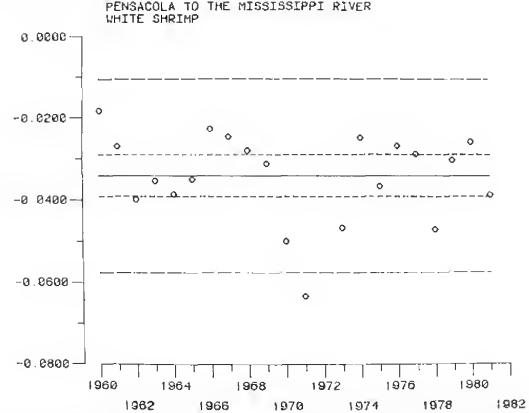


Figure 21. Mean (solid line) size composition index d (open circles) for reported May-August catches (inshore and offshore combined) of white shrimp from Pensacola to the Mississippi River (statistical areas 10–12 combined), 1960–1981 (data from Table 8, and Caillouet and Koi 1981). The 95% confidence limits are shown for the mean by short dashes and for individual values of d by long dashes.

continued trend of decreasing size. From 1979 to 1981, the index moved in a direction indicating increasing size of brown shrimp, but such variation was well within expected levels of variability in the index. The size composition index for white shrimp catches from the Mississippi River to Texas in May-August 1981 showed no significant departure from the trend of decrease in size (Figure 19). The size composition index for white

shrimp catches from the other two coastal areas in May-August 1981 fell within the 95% confidence limits for individual levels of d (Figures 17 and 21), showing that there was no significant departure in 1981 from the expected size composition. Thus the May-August 1981 size composition index was not a significant outlier in the 1960 to 1981 time series for either species in any of the three coastal areas.

May-August cumulative ex-vessel value of catch by size category

Caillouet and Koi (1981) used the logarithmic form of the following model to estimate parameters g and h by linear regression for each species, coastal area, and year from 1960 to 1978, and we updated this through 1981 (Tables 9–11):

$$\hat{D}_i = g(\exp h C_i) \quad (3)$$

where D_i = cumulative ex-vessel value (dollars) of catch in the i th size category. The ex-vessel values of the catches in each size category were cumulated starting with the size category of smallest shrimp and continuing toward the size category of largest shrimp, as was the case for cumulative pounds by size category, as described in the previous section. An example of the relationship between D and C is shown in Figure 22A, for brown shrimp from the Texas coast in 1981. An example of the fitted logarithmic form of model 3 is shown in Figure 22B. Very good fits were indicated by the very high coefficients of determination for each year (Tables 9–11, see also Caillouet and Koi 1981). All slopes, h , were negative, reflecting the construction of model 3 by cumulating ex-vessel value of catch from small-shrimp to large-shrimp size categories (Caillouet and Koi 1981). The slope, h , of each straight line is a simple index of the ex-vessel value composition of the May-August catch.

To determine whether there were significant trends in ex-vessel value composition of the May-August catch, we calculated the linear regression of h on the last two digits of each year from 1960 to 1981, for both species, and for each of the three coastal areas (Table 5). Only the upward trends in h for brown shrimp from the Texas coast (Figure 23) and for brown shrimp from Pensacola to the Mississippi River (Figure 27) were significant (Table 5). These upward trends indicated that ever increasing proportions of the ex-vessel value of the May-August catch of brown shrimp were represented by the size categories of smaller shrimp from these two coastal areas. The lack of significant trends in h for brown shrimp from the Mississippi River to Texas (Figure 25)

TABLE 9.

Parameter estimates^a of the linear regressions of transformed cumulative ex-vessel value (dollars) of catch, $\ln D$, on count, C , for reported May-August catches (inshore and offshore combined) of brown shrimp and white shrimp from the Texas coast (statistical areas 18–21 combined), 1979–1981.

Year	Brown Shrimp ^b			White Shrimp ^b		
	g	h	r^2	g	h	r^2
1979	80,877,806	-0.03648	0.981	10,839,636	-0.03306	0.940
1980	109,104,860	-0.04202	0.978	13,595,100	-0.05468	0.975
1981	195,936,268	-0.05388	0.969	8,313,905	-0.05042	0.990

^a $\ln(g) =$ intercept, $h =$ slope, and $r^2 =$ coefficient of determination.

^b Results of similar analyses of data from 1960 to 1978 can be found in Caillouet and Koi (1981).

TABLE 10.

Parameter estimates^a of linear regressions of transformed cumulative ex-vessel value (dollars) of catch, $\ln D$, on count, C , for reported May-August catches (inshore and offshore combined) of brown shrimp and white shrimp from the Mississippi River to Texas (statistical areas 13–17 combined), 1979–1981.

Year	Brown Shrimp ^b			White Shrimp ^b		
	g	h	r^2	g	h	r^2
1979	91,927,428	-0.01820	0.994	47,213,480	-0.06460	0.997
1980	40,696,392	0.00972	0.984	23,881,389	-0.04026	0.973
1981	78,311,890	-0.01689	0.980	43,460,368	-0.05200	0.960

^a $\ln(g) =$ intercept, $h =$ slope, and $r^2 =$ coefficient of determination.

^b Results of similar analyses of data from 1960 to 1978 can be found in Caillouet and Koi (1981).

TABLE 11.

Parameter estimates^a of linear regressions of transformed cumulative ex-vessel value (dollars) of catch, $\ln D$, on count, C , for reported May-August catches (inshore and offshore combined) of brown shrimp and white shrimp from Pensacola to the Mississippi River (statistical areas 10–12 combined), 1979–1981.

Year	Brown Shrimp ^b			White Shrimp ^b		
	g	h	r^2	g	h	r^2
1979	41,494,855	0.02142	0.874	3,000,562	-0.04246	0.958
1980	35,357,108	-0.03169	0.967	809,434	-0.03933	0.921
1981	32,078,930	-0.02267	0.899	1,481,447	-0.05701	0.938

^a $\ln(g) =$ intercept, $h =$ slope, and $r^2 =$ coefficient of determination.

^b Results of similar analyses of data from 1960 to 1978 can be found in Caillouet and Koi (1981).

and for white shrimp from all three coastal areas (Figures 24, 26, and 28) indicated that the ex-vessel value composition of these catches exhibited no significant trend. In these cases, the mean of the indices from 1960 to 1981 was calculated as a horizontal line through the points (Figures 24, 25, 26, and 28). No data point for 1972 was included in calculation of the mean h for white shrimp from Pensacola to the Mississippi River (Figure 28), as in the previous section concerning size composition.

The levels of h for brown shrimp and white shrimp catches from all three coastal areas in May-August 1981 fell within the 95% confidence bands or confidence limits for individual levels of h (Figures 23–28), indicating that there was no significant departure in 1981 from the expected ex-vessel value composition. Thus, the ex-vessel value composition indices for May-August 1981 were not significant outliers in the 1960–1981 time series.

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simple correlation coefficients, r , for the relationships among indices^a b, d and h and catch^b for May-August catches (inshore and offshore combined) of brown shrimp and white shrimp from the Texas Coast (statistical area 18-21 combined), the Mississippi River to Texas (statistical areas 17-18 combined), and Pensacola to the Mississippi River (statistical areas 10-12 combined). 1960-1961 indices b, d and h are defined in the text.

Coastal Area/Species	Texas Coast						Mississippi River to Texas						Panhandle to the Mississippi River								
	Brown Shrimp			White Shrimp			Brown Shrimp			White Shrimp			Brown Shrimp			White Shrimp					
	b	d	h	catch	b	d	h	catch	b	d	h	catch	b	d	h	catch	b	d	h		
Texas Coast																					
Brown Shrimp	b	1,000	-0.114	0.187	-0.157	0.123	0.221	-0.479 ^d	0.897 ^j	-0.233	0.230	-0.565 ^j	0.753 ^d	-0.186	0.065 ^j	-0.350 ^d	0.868 ^d	-0.333	-0.169	-0.493 ^d	
Brown Shrimp	d	1,000	0.987 ^j	0.018	-0.096	0.421	0.355	0.182	-0.347	0.507 ^j	0.295	0.474 ^j	-0.227	0.096	-0.167	0.184	-0.456 ^d	0.520 ^d	-0.441 ^d	-0.204	-0.462 ^d
Brown Shrimp	h	1,000	-0.007	-0.028	0.440 ^j	0.389	0.117	-0.233	0.54 ^j	0.360	0.430 ^j	-0.164	0.127	-0.011	0.115	0.374	0.525 ^d	-0.126	0.133	-0.295	-0.412
Brown Shrimp	catch	1,000	-0.210	0.083	0.074	-0.109	-0.249	0.53 ^j	0.084	0.616 ^j	-0.241	0.178	0.031	0.370	-0.241	0.130	0.073	0.560 ^d	0.056	-0.117	0.119
White Shrimp	b	1,000	0.285	0.424 ^j	-0.523 ^d	0.424 ^j	0.323	-0.333	0.704 ^j	0.217	-0.041	-0.533	0.565 ^d	-0.168	0.143	0.016	0.184	0.589 ^d	-0.107	0.080	-0.141
White Shrimp	d	1,000	0.075	0.083	-0.063	0.249	-0.163	0.066	0.519	0.247	0.030	0.089	-0.166	0.143	0.016	0.184	0.098	0.202	0.094	0.115	-0.289
White Shrimp	h	1,000	0.900	0.940 ^j	-0.143	0.315	-0.110	0.042	0.291	0.397	0.030	0.118	-0.107	0.219	0.029	0.087	0.093	0.256	0.090	-0.129	-0.252
White Shrimp	catch	1,000	-0.270	-0.402	0.252	0.143	0.060	-0.24	-0.041	0.164	0.202	-0.444 ^d	-0.463 ^d	0.202	-0.202	-0.444 ^d	0.248	0.126	0.216	-0.247	0.219
Panhandle to the Mississippi River																					
Panhandle to the Mississippi River to Texas																					
Brown Shrimp	b	1,000	-0.331	0.188	-0.587 ^d	0.184 ^j	0.176	-0.224	0.176	0.131	-0.226	-0.489 ^d	0.593 ^j	-0.216	0.166	-0.354 ^d	0.894 ^d	-0.435 ^d	-0.216	-0.531	-0.099
Brown Shrimp	d	1,000	-0.331	0.188	-0.587 ^d	0.184 ^j	0.176	-0.224	0.176	0.131	-0.226	-0.489 ^d	0.593 ^j	-0.216	0.166	-0.354 ^d	0.894 ^d	-0.435 ^d	-0.216	-0.531	-0.099
Brown Shrimp	h	1,000	-0.161	0.161	-0.223	0.166	0.166	-0.223	0.166	0.131	-0.226	-0.489 ^d	0.593 ^j	-0.216	0.166	-0.354 ^d	0.894 ^d	-0.435 ^d	-0.216	-0.531	-0.099
White Shrimp	b	1,000	-0.333	-0.454 ^d	-0.334 ^d	-0.172	-0.028	-0.035 ^j	-0.172	-0.035 ^j	-0.172	-0.035 ^j	-0.172	-0.035 ^j	-0.172	-0.035 ^j	-0.172	-0.035 ^j	-0.172	-0.035 ^j	
White Shrimp	d	1,000	-0.333	-0.454 ^d	-0.334 ^d	-0.172	-0.028	-0.035 ^j	-0.172	-0.035 ^j	-0.172	-0.035 ^j	-0.172	-0.035 ^j	-0.172	-0.035 ^j	-0.172	-0.035 ^j	-0.172	-0.035 ^j	
White Shrimp	h	1,000	-0.160	0.160	-0.223	0.166	0.166	-0.223	0.166	0.131	-0.226	-0.489 ^d	0.593 ^j	-0.216	0.166	-0.354 ^d	0.894 ^d	-0.435 ^d	-0.216	-0.531	-0.099
Panhandle to the Mississippi River to the Mississippi River																					
Panhandle to the Mississippi River to the Mississippi River																					
Brown Shrimp	b	1,000	1,000	-0.568 ^d	-0.365	-0.443 ^d	1,000	1,000	-0.963 ^d	1,000	1,000	-0.635	-0.443 ^d	1,000	1,000	-0.809 ^d	1,000	-0.563 ^d	1,000	-0.142	
Brown Shrimp	d	1,000	1,000	-0.568 ^d	-0.365	-0.443 ^d	1,000	1,000	-0.963 ^d	1,000	1,000	-0.635	-0.443 ^d	1,000	1,000	-0.809 ^d	1,000	-0.563 ^d	1,000	-0.142	
Brown Shrimp	h	1,000	1,000	-0.568 ^d	-0.365	-0.443 ^d	1,000	1,000	-0.963 ^d	1,000	1,000	-0.635	-0.443 ^d	1,000	1,000	-0.809 ^d	1,000	-0.563 ^d	1,000	-0.142	
White Shrimp	c	1,000	1,000	-0.568 ^d	-0.365	-0.443 ^d	1,000	1,000	-0.963 ^d	1,000	1,000	-0.635	-0.443 ^d	1,000	1,000	-0.809 ^d	1,000	-0.563 ^d	1,000	-0.142	
White Shrimp	h	1,000	1,000	-0.568 ^d	-0.365	-0.443 ^d	1,000	1,000	-0.963 ^d	1,000	1,000	-0.635	-0.443 ^d	1,000	1,000	-0.809 ^d	1,000	-0.563 ^d	1,000	-0.142	

The latitudes b, d, and h are shown in Tables 2-4, 6-8, and 9-11, respectively, for the years 1979-1981, and in Culloue and Koi (1981) for the years 1960-1978.

for the year 1895-96.

Data for 1972 were excluded from all correlation analyses involving indices b, d, and h for white shrimp from Pensacola to the Mississippi.

River (see *Calhoue* and *Kodiak* [1-28]).

The correlation coefficient was significantly different from zero at the 95% level of confidence.

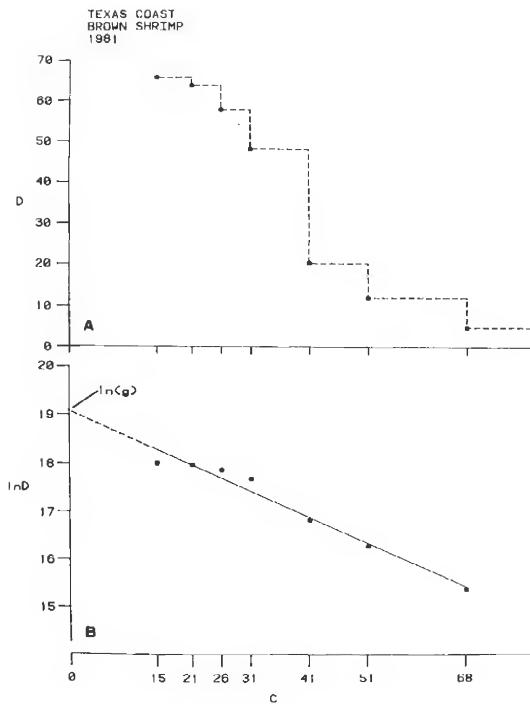


Figure 22. Relationship between the cumulative ex-vessel value (millions of dollars) of catch, D, and count, C, for reported May-August catch (inshore and offshore combined) of brown shrimp from the Texas coast (statistical areas 18–21 combined) in 1981 (graph A). In graph B, the line was fitted by linear regression (see Table 9).

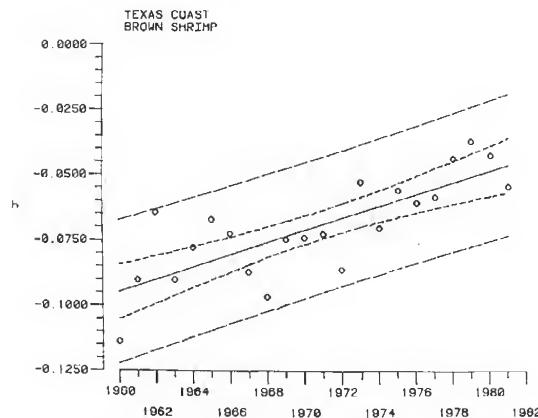


Figure 23. Trend (solid line) in the ex-vessel value composition index h (open circles) for reported May-August catches (inshore and offshore combined) of brown shrimp from the Texas coast (statistical areas 18–21 combined), 1960–1981 (data from Tables 5 and 9, and Caillouet and Koi 1981). The 95% confidence bands are shown for the trend line by short dashes and for individual values of h by long dashes.

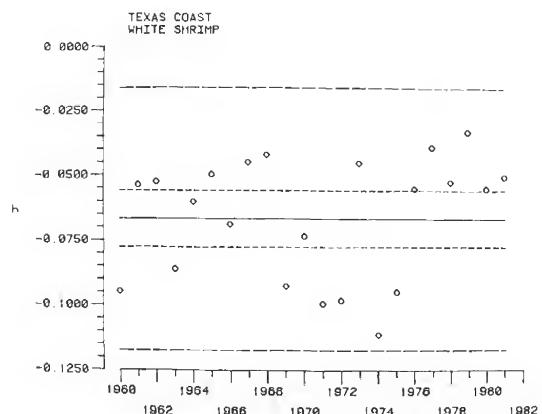


Figure 24. Mean (solid line) ex-vessel value composition index h (open circles) for reported May-August catches (inshore and offshore combined) of white shrimp from the Texas coast (statistical areas 18–21 combined), 1960–1981 (data from Table 9, and Caillouet and Koi 1981). The 95% confidence limits are shown for the mean by short dashes and for individual values of h by long dashes.

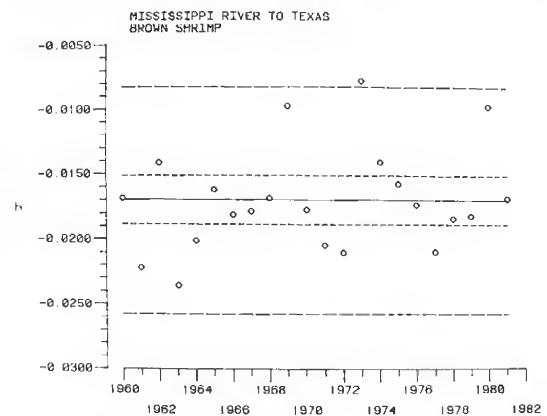


Figure 25. Mean (solid line) ex-vessel value composition index h (open circles) for reported May-August catches (inshore and offshore combined) of brown shrimp from the Mississippi River to Texas (statistical areas 13–17 combined), 1960–1981 (data from Table 10, and Caillouet and Koi 1981). The 95% confidence limits are shown for the mean by short dashes and for individual values of h by long dashes.

Tests for correlations among indices b, d, and h, and the weight of the May-August catches

In order to determine if indices b, d, and h (Tables 2–4, 6–8 and 9–11, respectively; and Caillouet and Koi 1981) were closely related to one another, and if any of these indices were closely related to the total weight of the May-August catch (Figures 2–7), we calculated the simple correlation coefficients, r , for the relationships between all possible pairs of indices b, d, and h and catch, for both

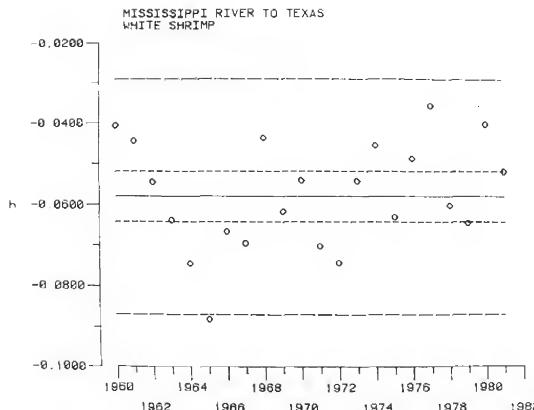


Figure 26. Mean (solid line) ex-vessel value composition index h (open circles) for reported May-August catches (inshore and offshore combined) of white shrimp from the Mississippi River to Texas (statistical areas 13–17 combined), 1960–1981 (data from Table 10, and Caillouet and Koi 1981). The 95% confidence limits are shown for the mean by short dashes and for individual values of h by long dashes.

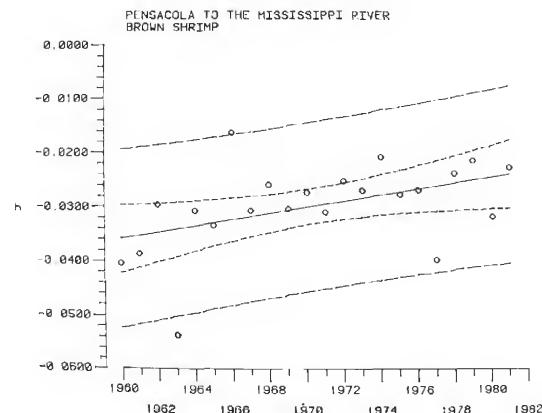


Figure 27. Trend (solid line) in the ex-vessel value composition index h (open circles) for reported May-August catches (inshore and offshore combined) of brown shrimp from Pensacola to the Mississippi River (statistical areas 10–12 combined), 1960–1981 (data from Tables 5 and 11, and Caillouet and Koi 1981). The 95% confidence bands are shown for the trend line by short dashes and for individual values of h by long dashes.

species and each of the three coastal areas (Table 12). Each year provided one observation for each index and weight of catch. In the case of all correlation analyses involving indices b , d , and h for white shrimp from Pensacola to the Mississippi River, one less observation was available, because the data for 1972 had to be excluded (Caillouet and Koi 1981).

The reader is cautioned that significant correlations (those significantly greater or less than zero) do not necessarily reflect cause and effect relationships. However, a

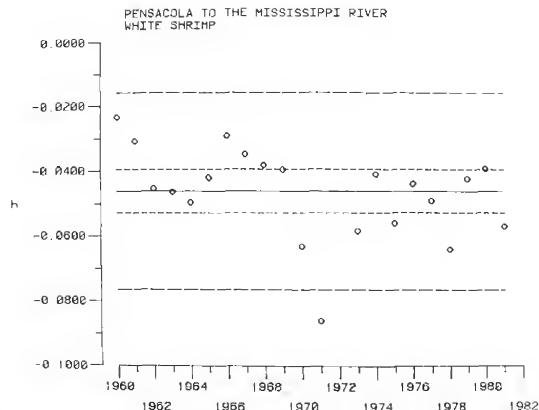


Figure 28. Mean (solid line) ex-vessel value composition index h (open circles) for reported May-August catches (inshore and offshore combined) of white shrimp from Pensacola to the Mississippi River (statistical areas 10–12 combined), 1960–1981 (data from Table 11, and Caillouet and Koi 1981). The 95% confidence limits are shown for the mean by short dashes and for individual values of h by long dashes.

number of general patterns emerged among the significant correlations (Table 12). For example, there were significant positive correlations between the May-August brown shrimp catches in all three coastal areas. Such results suggest that there was a region-wide influence on the May-August catches of brown shrimp, because there was a tendency for the catches to vary in the same direction from year to year in the three coastal areas. This could be explained by region-wide influences on brown shrimp recruitment, or by parallel changes in fishing effort in each of the three coastal areas, or both. The May-August white shrimp catches were not significantly correlated among the coastal areas, with the one exception: the white shrimp catches from the Mississippi River to Texas and from Pensacola to the Mississippi River were significantly correlated with each other. We offer no explanation for this correlation.

There were significant positive correlations between the ex-vessel price spread indices, b , for brown shrimp in all three coastal areas (Table 12). The same was true for price spread indices for white shrimp in all three coastal areas. Also, there were significant positive correlations between the price spread indices for the two species. This suggests a region-wide influence on price spread, because there was a tendency for the price spread to vary in the same direction from year to year in both species and in all three coastal areas. In most cases, but not all, there were significant negative correlations between the price spread index and the weight of the May-August catches (i.e., the current local supply of shrimp), both between species and between coastal areas, suggesting that price spread was wider when the catch was high, and narrower when the catch was low. Again, a regional influence was apparent, because the correlations existed between species and between coastal areas in most cases.

Among the highest of the significant correlations were the positive correlations between indices of size composition, d, and ex-vessel value composition, h, for a given species within a given coastal area. This was to be expected, because the ex-vessel value composition of the catch reflects, to a large extent, the size composition of the catch. This is particularly important, because it reinforces the general consensus that the size composition of the catch plays a major role in determining the ex-vessel value of the catch (Caillouet and Patella 1978).

While there were a number of additional significant correlations depicted in Table 12, they did not follow any particular pattern; therefore we did not attempt an explanation for these cases. However, the absence of significant correlations is noteworthy in at least one case. For example, within a given species and coastal area, there were no significant correlations between the weight of the May-August catch and the size composition index. This indicates that the size composition of the catch is not the major factor affecting the weight of the catch, or vice versa. Year to year variations in recruitment, fishing effort or both, may be overriding factors in this regard. That is not to say that size composition has no effect on the weight of the catch. As might be expected, differences in fishing regulations and fishing strategy among the three coastal areas have had pronounced effects upon the size composition of the catches (Caillouet et al. 1980, Caillouet and Koi 1980).

DISCUSSION

Based upon our analyses of the best catch statistics available from the TIMS in February 1982, we detected significant trends of decrease in size of brown shrimp in the reported May-August catches from the three coastal areas over the years 1960 to 1981. This corroborates similar findings by Caillouet and Koi (1980) for the period 1960–1978. In addition, Caillouet et al. (1980) detected significant decreases in size of brown shrimp in reported annual catches from Texas and Louisiana from 1959 to 1976, and Caillouet and Koi (1980) detected significant decreases in size of brown shrimp in reported annual landings from the northern Gulf from 1961 to 1977.

In 1981, the size composition index for the May-August brown shrimp catch in each of the three coastal areas did not depart significantly from that expected, based on the general trends of decrease in size from 1960 to 1981 (Figures 16, 18, and 20). It barely fell out of the 95% confidence bands for the trend lines, and it was well within the 95% confidence intervals for the individual levels of the index predicted for each coastal area for 1981, based on the entire 1960 to 1981 time series. Despite these trends of decrease in size, the total weight of the May-August catch of brown shrimp from all three coastal areas was higher in 1981 than in 1980 (Figures 2, 4, and 6), and the ex-vessel value of the May-August catch of brown shrimp from the Texas coast

was at an all time high (Figure 2). The higher catches of brown shrimp in 1981, coupled with the continued increase in ex-vessel price spread, enhanced the ex-vessel value of the brown shrimp catches, particularly in Texas where brown shrimp continued to be larger than those in catches from the Mississippi River to Texas and Pensacola to the Mississippi River.

The May-August brown shrimp catches in all three coastal areas showed a tendency to vary in the same direction from year to year. Also, the lack of a significant correlation, using the 1960 to 1981 time series, between the total weight and the size composition of the May-August catch of brown shrimp within each of the three coastal areas, suggested that size composition was not the major determinant of weight of the catch or vice versa. These findings, coupled with the fact that there were no detectable departures in 1981 from the trends of decreasing size in brown shrimp in the May-August catches from the three coastal areas during 1960 to 1981, suggested that the observed increases in brown shrimp catch from all three coastal areas reflected some region-wide influence.

According to Jones and Zweifel (1982), there was more fleet movement in June-August 1981 than in a comparable period in 1980, and they attributed this to the Texas Closure. The change in mobility included shifts to areas away from the Texas coast during the closure and back to the Texas coast thereafter. Klima et al. (1982) indicated that recruitment from Texas bays to the offshore fishery appeared to be average to good in 1981, but not so good as to account for the outstanding abundance levels found offshore of Texas. According to Charles J. White (Louisiana Department of Wildlife and Fisheries, Lake Charles, Louisiana, personal communication, March 1982), brown shrimp recruitment in Louisiana, both west and east of the Mississippi River, was near record levels in 1981. Also, J. Y. Christmas (Gulf Coast Research Laboratory, Ocean Springs, Mississippi, personal communication, March 1982) indicated that there was good brown shrimp recruitment in 1981 in the area of Mississippi Sound off the coast of Mississippi.

There were no significant trends in size composition of reported May-August catches of white shrimp from the Texas coast and from Pensacola to the Mississippi River from 1960 to 1981, a result similar to that reported for May-August catches from 1960 to 1978 by Caillouet and Koi (1981). However, there was a significant trend of decrease in size of white shrimp in the May-August catch from the Mississippi River to Texas from 1960 to 1981. The size composition of the May-August 1981 catch of white shrimp in the three coastal areas showed no significant departure from that expected based on 1960–1981 trends or mean levels (Figures 17, 19, and 21). On the other hand, Caillouet et al. (1980) and Caillouet and Koi (1980) detected decreases in size of white shrimp in reported annual catches and landings, respectively, from the northern Gulf of Mexico.

Therefore, the observed trends of decrease in size of white shrimp in the annual catches and landings from the northern Gulf must reflect an overriding influence of catches in months other than May-August. The low percentages of the annual white shrimp catches taken in May-August (Table 1) corroborate this. While the ex-vessel price spread for white shrimp in the May-August catch from the Mississippi River to Texas and from Pensacola to the Mississippi River increased from 1960-1981, no such trend was detected in price spread for white shrimp from the Texas coast (Table 5).

Our analyses did not demonstrate immediate and detectable increases in size of brown shrimp or white shrimp in the May-August catch concomitant with the Texas Closure in 1981. However, the total weight and ex-vessel value of the May-August catches of both species in each coastal area were higher in 1981 than in 1980, with one exception: white shrimp from the Texas coast exhibited a slight decrease in weight of May-August catch in 1981 as compared to 1980, but there was nevertheless an increase in ex-vessel value of this catch.

The magnitude of the increase in weight of the May-August catch of brown shrimp between 1980 and 1981 was greater for the Mississippi River to Texas (18.6 million pounds, or 94%, Figure 4) than for either the Texas coast (12.1 million pounds, or 69%, Figure 2) or Pensacola to Mississippi River (3.2 million pounds, or 45%, Figure 6). This occurred despite the fact that approximately half of statistical area 17, which is located within the Mississippi River to the Texas coastal area, was closed to shrimping during the Texas Closure. Also, the magnitude of the increase in ex-vessel value of the May-August catch of brown shrimp between 1980 and 1981 was greater for the Mississippi River to Texas (22.6 million dollars, or 66%, Figure 4) than for either the Texas coast (18.2 million dollars, or 38%, Figure 2) or Pensacola to the Mississippi River (0.9 million dollars, or 5%, Figure 6). Nonetheless, in May-August 1981, the Texas coast continued to produce brown shrimp catches of higher ex-vessel value than the other two coastal areas, because these catches were represented by larger shrimp which brought a higher price than in the other two coastal areas. Our findings are consistent with the findings of Poffenberger (1982) who estimated an increase in revenue of 21.5 million dollars to the Gulf of Mexico brown shrimp fishery during May-August 1981.

We concluded that the increases in brown shrimp catches in May-August 1981, as compared to May-August 1980, appeared to be due to a region-wide influence, perhaps good recruitment in 1981, or increased fishing effort, or both. This finding is not necessarily inconsistent with those of Klima et al. (1982), Nichols (1982), or Matthews (1982),

because these authors dealt only with offshore catches, and concluded that offshore abundance and yield of brown shrimp was enhanced by the closure. Our analyses dealt with inshore and offshore catches combined. It was obvious that the continued increase in ex-vessel price spread among size categories of shrimp continued to enhance the ex-vessel value of the catches, especially on the Texas coast.

The reader is reminded that our analyses dealt only with the May-August catches. For the Texas coast, the May-August period produces a smaller proportion (averaging 58%) of the calendar year annual brown shrimp catch from the Texas coast, than does a similar period for the Mississippi River to Texas (81%), or for Pensacola to the Mississippi River (83%). Thus, the May-August time interval appears to be too brief a period to show the full effects of the Texas Closure on size composition or yield of the brown shrimp. An examination of the annual catches, fishing effort, and recruitment in 1981, as compared to earlier years, might be useful in more fully assessing the impacts of the Texas Closure. An analysis applying our approach to biological year catch statistics for brown shrimp might also be useful in further assessments of impacts of the Texas Closure or other management strategies. For that purpose, we would recommend a biological year beginning in May of one year and ending in April of the following year, based upon our examination of the weight and size composition of monthly catches of brown shrimp.

ACKNOWLEDGMENTS

We are especially grateful to those who designed and implemented the gathering of data on weight and ex-vessel value of shrimp catches by statistical area, species and size category, since they have made our analyses possible. Notable among them are Charles H. Lyles, Director, Gulf States Marine Fisheries Commission (formerly of the USFWS); George W. Rounsefell (deceased; formerly Director, Galveston Biological Laboratory, BCF, USFWS); Joseph H. Kutkuhn, Director, Great Lakes Fisheries Laboratory, USFWS, Ann Arbor, Michigan (formerly Assistant Director, Galveston Biological Laboratory, BCF, USFWS); George W. Snow (retired; formerly Chief, Division of Statistics and Market News, NMFS, New Orleans, Louisiana); and TIMS.

The manuscript was reviewed by Dr. Edward F. Klima, Director, NMFS Southeast Fisheries Center (SEFC), Galveston Laboratory, and by Dr. Albert C. Jones, Dr. Joseph Powers and Mr. John R. Poffenberger, NMFS, SEFC, Miami, Florida, who provided many helpful suggestions. Beatrice Richardson, clerk-typist, NMFS, SEFC, Galveston Laboratory, typed the manuscript.

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MULTILINEAR MODELS FOR THE PREDICTION OF BROWN SHRIMP HARVEST IN MISSISSIPPI WATERS

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ABSTRACT A multilinear regression analysis of water temperature, salinity, and number of postlarval brown shrimp in nursery areas was used to predict the June and July commercial harvest of brown shrimp in Mississippi waters. A total of 80.2% of the variation in harvest was accounted for by this model. When an effort variable was added to the equation, the amount of variation explained by these parameters increased to 85.4%. The coefficients of the two multilinear equations were recalculated exclusive of the data set for the last year to test the predictive capabilities of the models. For that year, the first model showed a percent error of 38.2%, and the second model, 35.3%.

INTRODUCTION

Prediction of commercial brown shrimp harvest from a postlarval index has been used with various degrees of success in several areas of the Gulf of Mexico and Atlantic coasts (Christmas and VanDevender 1981). Williams (1969) tried unsuccessfully to correlate the number of brown shrimp postlarvae and the subsequent commercial harvest in North Carolina. Baxter (1962) and Berry and Baxter (1969) examined the number of postlarval shrimp relative to commercial and bait shrimp harvest in Galveston Bay, Texas; however, a juvenile index gave a better reflection of size of shrimp stocks. St. Amant et al. (1966), and Gaidry and White (1973) also examined postlarval/harvest relationships with mixed success for areas in Louisiana.

Postlarval brown shrimp data from Mississippi waters from the years 1963–1964 and 1971–1976 were examined by Christmas and VanDevender (1981) relative to predicting commercial harvest from Gulf Coast Shrimp Data (U.S. Department of Commerce 1963 et seq.) for areas 11.1, 12.1, and 11.0 (Figure 1). They found a positive correlation between the number of postlarvae and resultant commercial harvest. After 1975, Gulf Coast Shrimp Data statistical areas 11.1 and 12.1 were combined and designated as area 11.1. To avoid confusion, these areas will now be referred to only as Mississippi waters. The samples discussed by Christmas and VanDevender (1981) differed from other studies from the Gulf of Mexico in that their samples of postlarvae were obtained from protected nearshore estuarine areas (or 'nursery' areas) rather than from open passes into the estuary. The results from Mississippi waters may provide a better indication of the number of postlarvae that will survive to harvestable size.

Temperature and salinity have been noted to have an appreciable effect on growth and survival of brown shrimp (Gunter et al. 1964, Zein-Eldin and Aldrich 1965, Christmas and VanDevender 1981). Barrett and Gillespie (1973)

also found water temperature had an effect on subsequent brown shrimp harvest in Barataria Bay, Louisiana. In this study, temperature and salinity were examined together with a postlarval index in developing predictive models of the commercial harvest of brown shrimp in Mississippi waters.

MATERIALS AND METHODS

Data Base

Data on number of postlarvae, temperature, and salinity were obtained for 1963–1964 from Christmas et al. (1966), 1966 and 1967 (unpublished data), 1971–1973 from Christmas et al. (1976), and 1973–1981 from an ongoing assessment and monitoring program in Mississippi waters (PL 88–309, Projects 2–215–R and 2–296–R). The beam plankton trawl (BPL) used to collect postlarvae in all of the

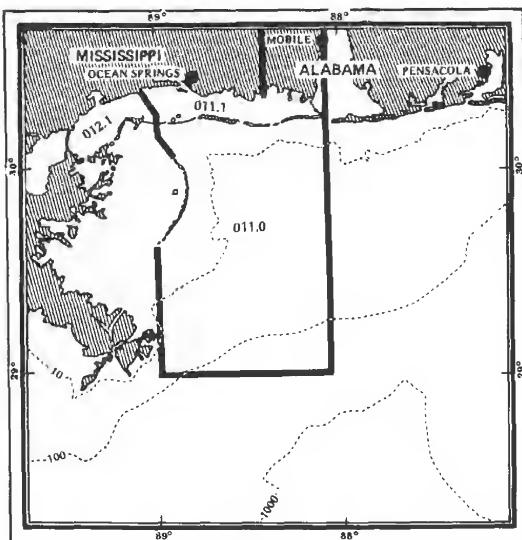


Figure 1. Location of statistical areas used for Gulf Coast Shrimp Data.

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studies was described by Christmas et al. (1966). Beam plankton trawl samples were taken twice a month at four stations (1, 4, 11, and 13, detailed station description and location in Christmas et al. 1966).

Commercial harvest data of brown shrimp for 1963–1964, 1966–1967, and 1971–1981 were obtained from the Gulf Coast Shrimp Data for June and July in Mississippi waters and summarized in Table 1.

Model Development

Christmas and VanDevender (1981) discussed several relationships between number of postlarvae and commercial harvest in Mississippi waters; however, they did not combine all of these relationships in a single equation. The first step of the present investigation was to define the relationship between these two parameters. Identification of which values were to be used in the calculation of a postlarval index had to be determined. These results were then put in the form of variable definitions. Monthly catch-per-unit-effort values of brown shrimp postlarvae from stations 1, 4, 11, and 13 are shown in Table 2 (for 1963–1964, 1966–1967, and 1971–1981). From these data the following guidelines were established for the calculation of the postlarval index:

- 1) The average catch-per-unit-effort values for March, April, and May are always included in the calculations;
- 2) the February CPUE value is included in the index if the mean catch is greater than 5;
- 3) the June CPUE value is included in the index if the mean catch is greater than 10.

The months of March, April, and May were always used in the calculation of the postlarval index because these were the months of peak abundance of postlarvae in the nursery area. Because postlarvae arrive in some years as early as

February and/or continue to be recruited into June, guidelines (2) and (3) were established. For example, using the information from Table 2, the 1981 postlarval index =

$$\frac{(10.8 + 358.0 + 13.0)}{3} = 127.3.$$

The relationship between the postlarval index (X) and commercial harvest in Mississippi waters (Y) was described by a least squares regression analysis. Harvest data were defined as the catch in June and July from Mississippi waters for 1963–1964, 1966–1967, and 1971–1981. For ease in data manipulation, these values were scaled by a divisor of 100,000. The resulting equation was $Y = 0.331 + 0.01X$; $r = 0.81$; $N = 10$. Data from 1967, 1975, 1977, 1979, and 1980 were not included in the regression analysis because of the extremely low catch of brown shrimp postlarvae in these years (less than 60, Table 2) suggesting that for those years, the BPL samples were not representative of the number of postlarvae in the nursery area.

With the relationship between postlarvae and commercial harvest established for all available data, several other predictor variables were examined in an attempt to enhance the predictive capabilities of a brown shrimp commercial harvest model for Mississippi waters. Variables used included:

1) Salinity (X_1). The salinity data used for this variable were obtained at BPL stations 1 and 11 for March, April, and May. These two stations were used because they gave the best indications of inshore nursery conditions in Mississippi waters. This variable was calculated as the average salinity of stations 1 and 11 for March through May (peak months of postlarvae abundance in the nursery area).

2) Interaction index (X_2). Both temperature and salinity are critical to the survival and growth of postlarvae in nursery

TABLE I.
Number of pounds of brown shrimp caught and number of trips from Mississippi waters during June and July
(Gulf Coast Shrimp Data).

Year	June		July		June & July	
	lbs	No. of Trips	lbs	No. of Trips	lbs	No. of Trips
1963	475,286	711.3	330,459	640.0	805,745	1351.3
1964	617,902	972.0	384,799	990.0	1,002,701	1962.0
1966	494,550	—	703,355	2011.0	1,197,905	—
1967	2,085,374	2376.0	806,947	2008.0	2,892,321	4384.0
1971	119,403	324.0	1,667,752	2604.0	1,787,155	2928.0
1972	501,845	851.2	704,832	1366.0	1,206,677	2217.2
1973	199,981	598.0	310,121	1206.0	510,102	1804.0
1974	618,837	971.3	431,925	1351.3	1,050,762	2322.6
1975	366,808	655.0	584,207	1311.0	951,015	1966.0
1976	1,224,605	1665.6	858,623	2329.5	2,088,228	3935.1
1977	2,755,454	2310.8	675,028	1383.1	3,450,482	3693.9
1978	668,982	556.1	261,824	562.3	930,806	1118.1
1979	1,395,295	1751.4	850,213	2343.7	2,245,509	4095.1
1980	696,083	624.1	942,344	1233.5	1,638,427	1857.6
1981	1,201,705	1332.0	393,524	1074.0	1,595,029	2406.0

TABLE 2.

Monthly catch-per-unit-effort values of brown shrimp postlarvae from stations 1, 4, 11, and 13, and respective postlarval index values.

Year	Month					Postlarval index
	February	March	April	May	June	
1963	0.0	64.5	101.5	126.5	163.9	112.8
1964	12.8	157.5	167.8	57.5	121.0	103.8
1966	--	156.2	291.0	68.6	58.8	143.6
1967	13.8	82.5	164.6	4.6	10.9	55.3
1971	2.2	334.2	90.6	2.6	0.2	142.4
1972	4.1	236.2	153.3	33.8	13.4	109.2
1973	3.6	76.9	107.0	51.7	36.0	67.9
1974	7.8	174.9	227.2	40.4	65.8	103.2
1975	24.9	65.4	46.6	10.5	30.4	35.6
1976	5.0	269.5	150.1	50.1	84.6	138.6
1977	7.0	28.1	94.5	47.9	45.0	44.5
1978	0.0	36.9	353.4	105.2	33.3	132.2
1979	1.5	13.2	29.9	37.6	4.4	26.9
1980	1.9	4.5	18.4	27.1	5.2	16.7
1981	0.8	10.8	358.0	13.0	1.8	127.3

areas. The interaction variable was based on temperature and salinity values from stations 1, 4, 11, and 13 in March, April, and May (as a measure of the environmental conditions for postlarvae in Mississippi Sound). In the calculation of this index, the average salinity values from stations 1, 4, 11, and 13 were combined and an overall monthly mean was determined. The resulting value was then multiplied by the average monthly temperature from the same four stations. The products of the monthly mean temperature times mean salinity for March, April, and May were summed.

Example: Interaction Index for 1981

	Months		
	March	April	May
Salinity	21.9	15.0	21.2
Temperature	16.4	24.7	25.0
Salinity x Temperature	359.16	370.50	530.00
	$\Sigma = 1259.76$		

3) Postlarval index (X_3). The postlarval index was explained earlier in the text. Values of this parameter were given in Table 2 for 1963, 1964, 1966, 1967, and 1971–1981.

An assigned range of numbers for each index, a value of -1, 0, or 1 depending on how the respective parameter was to be weighted, dampened the variability of the salinity, interaction, and postlarval indices. The following criteria were used:

Salinity index:

- a) if the salinity index is greater than 14, then $X_1 = 0$
- b) if the salinity index is less than 14, but greater than 9, then $X_1 = 1$
- c) if the salinity is less than 9, then $X_1 = -1$

Interaction index:

- a) if the interaction index is greater than 900, then $X_2 = 0$
- b) if the interaction index is less than 900, but greater

than 650, then $X_2 = 1$

c) if the interaction index is less than 650, then $X_2 = -1$

Postlarval index:

- a) if the postlarval index is greater than 135, then $X_3 = 1$
- b) if the postlarval index is less than 135, but greater than 100, then $X_3 = 0$
- c) if the postlarval index is less than 100, but greater than 60, then $X_3 = -1$
- d) if the postlarval index is less than 60, then that year was not included in model construction.

RESULTS AND DISCUSSION

A summary of the calculations for the predictor variables is given in Table 3. All values were then transformed according to the outline above. We placed the predictor variables; salinity index (X_1), interaction index (X_2) and postlarval index (X_3) in the form of a multilinear regression equation using the \log_{10} of the June and July commercial harvest of brown shrimp $\times 10^{-5}$ from Mississippi waters as the dependent variable (Tables 2 and 3), giving:

Model 1

$$\log Y = 1.0189 - 0.2336(X_1) + 0.2226(X_2) + 0.2927(X_3)$$

where

$$F_{3,6} = 8.116 \quad (p < .05)$$

$$R^2 = 0.802$$

$$\text{Confidence Interval (95\%)} = 0.073$$

This model accounted for 80.2% of the variability of the June and July brown shrimp commercial harvest from Mississippi waters.

Christmas et al. (1966) found a significant correlation ($r = -.8018$, $p < .01$) between fishing effort and catch per 24 hour day of brown shrimp in Mississippi waters. To account for this relationship, we added an effort variable to the multilinear model. The only data available through 1981

TABLE 3.
Summary of the calculations used in the brown shrimp predictive harvest models.

Year	\log_{10} Harvest of Mississippi Sound for June + July 100,000	X				Number of Trips 1000
		X ₁ Salinity Index	X ₂ Interaction Index	X ₃ Postlarval Index	X ₄	
1963	0.906	17.1	1451.6	112.8		1.35
1964	1.001	6.4	591.8	103.8		1.96
1966	1.078	10.5	940.4	143.6		2.40
1967	1.461	18.5	910.4	55.3		4.38
1971	1.252	9.0	732.0	142.4		2.93
1972	1.082	14.7	1282.0	109.2		2.21
1973	0.708	6.6	624.7	67.9		1.80
1974	1.021	5.1	624.5	103.2		2.32
1975	0.978	5.4	508.4	35.6		1.97
1976	1.320	11.2	770.7	138.6		3.94
1977	1.535	5.2	552.1	44.5		3.69
1978	0.970	10.0	866.3	132.2		1.12
1979	1.350	2.4	290.3	26.9		4.10
1980	1.214	6.5	692.0	16.7		1.86
1981	1.203	16.8	1259.7	127.3		2.42

that provided some indication of effort were the number of fishing trips as reported in the Gulf Coast Shrimp Data. The number of trips made in Mississippi waters during June and July (X, values divided by 1000 in Table 3) was found to correlate with the commercial yield ($\ln Y \times 10^{-5}$) for the same time frame and area, for 1963–1964, 1967–1968, and 1971–1981. This relationship was described by $\ln Y = 0.663 + 0.185 X; r = 0.84; N = 15$.

The number of trips ($x 10^{-3}$) was included as another predictor variable (X_4) in the following multilinear regression equation:

Model 2

$$\log Y = 0.8611 - 0.1489 (X_1) + 0.1653 (X_2) + 0.1895 (X_3) + 0.0760 (X_4)$$

where

$$F_{4,5} = 7.300 (p < 0.05)$$

$$R^2 = 0.854$$

$$CI_{95} = 0.073$$

The amount of variability explained by the predictor variables increased to 85.4% when the number of trips was included in the model. However, information on the number of trips is not available until after the commercial harvest has already taken place. If a series of effort values were used beforehand to estimate the potential harvest, then the effort variable might increase the value of the model as a resource management tool.

These two multilinear models were then applied to the data used to construct the models, and the results were plotted against actual harvest (Figure 2). Brown shrimp harvest estimates for 1967, 1975, 1977, 1979, and 1980, because they were not included in model construction, were determined by the use of an assigned postlarval index value of 0.

Test of the Multilinear Models

To properly verify the predictive capabilities of the two multilinear regression models, it is necessary to have data that were not used in model construction. Since these additional data were not available, the equations were recalculated after excluding the 1981 data set. The 1981 data (Table 3) employed in these new equations provided an estimate of the June and July harvest of brown shrimp in Mississippi waters for 1981.

Model I: $\log Y = 0.9938 - 0.2253 (X_1) + 0.2059 (X_2) + 0.3095 (X_3)$

where

$$F_{3,5} = 22.469 (P < 0.005)$$

$$R^2 = 0.931$$

$$CI_{95} = 0.054$$

Model II: $\log Y = 0.8913 - 0.1697 (X_1) + 0.1693 (X_2) + 0.2393 (X_3) + 0.0505 (X_4)$

where

$$F_{4,4} = 20.99 (p < 0.01)$$

$$R^2 = 0.954$$

$$CI_{95} = 0.051$$

With these equations, Model I gave an estimate of 0.994 which converts to 986,279 pounds of brown shrimp harvested from Mississippi Sound in June and July 1981. Model II yielded an estimate of $\log Y = 1.014$ (1,032,761 lbs). The actual yield for June and July 1981 was 1,595,879 lbs ($\log Y = 1.203$), which showed the percent error of Model I (after conversion to pounds of harvest) to be 38.2% and Model II, 35.3%.

CONCLUSION

Commercial harvest of brown shrimp can be predicted with some confidence (accounting for 80.2% of the variability)

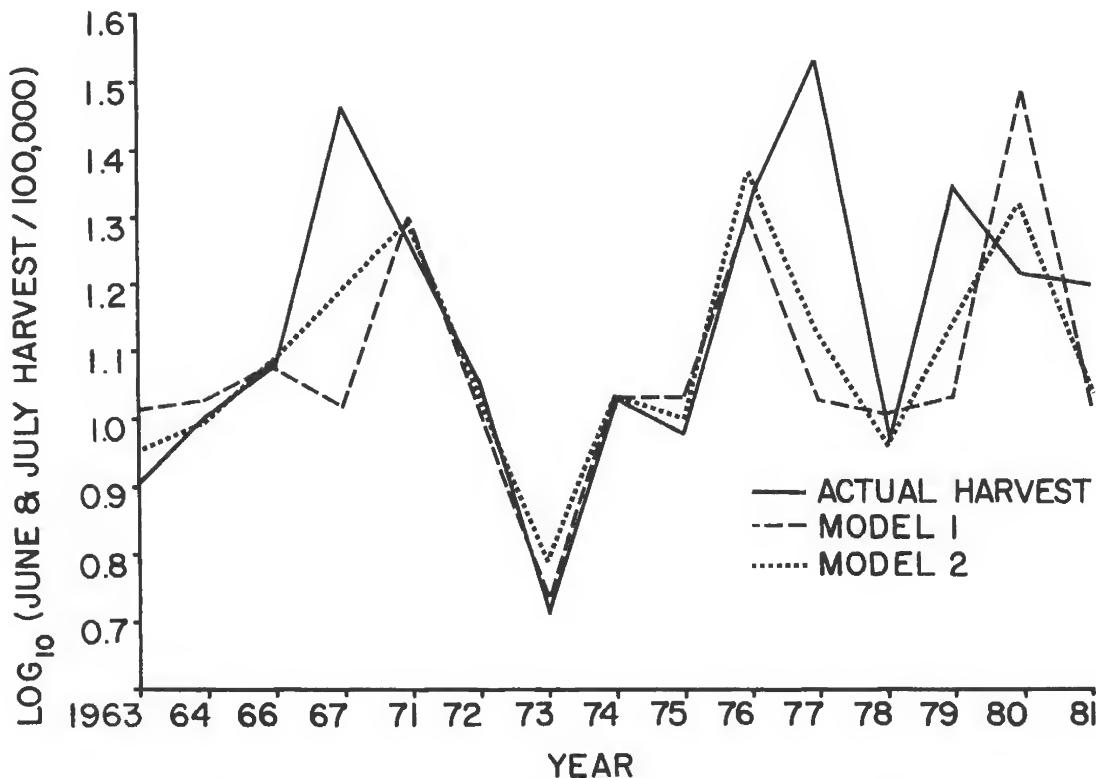


Figure 2. Predicted (Model 1 and 2) and actual June and July harvests of brown shrimp from Mississippi waters.

from indices of temperature, salinity, and number of post-larvae in the nursery ground areas of Mississippi Sound. When the number of trips were added to the first multilinear model as a measure of commercial effort, the amount of variability explained by the predictor variables increased to 85.4%. Although these models are the result of a preliminary study, they do indicate several areas where further work may improve their predictive capabilities. The examination of factors that influence the number of postlarvae, postlarval growth and survival, and evaluation of parameters that affect the nursery ground areas should help to refine the predictive capabilities of the models. Studies of currents, movement patterns of juveniles and adults, and influence of fishing

effort should also be addressed. The results of the present investigation indicate that predictive models of brown shrimp harvest in Mississippi Sound may be a practical management tool.

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AMPHIPODS OF THE FAMILY AMPELISCIDAE (GAMMARIDEA)

I. AMPELISCA BICARINATA, A NEW SPECIES OF AMPHIPOD FROM THE GULF OF MEXICO

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ABSTRACT A new species of the benthic amphipod genus *Ampelisca* Kroyer, is described and illustrated. Previous records of the Pacific species *Ampelisca cristoides* Barnard, 1954, from the western North Atlantic are now assignable to the proposed new species, *Ampelisca bicarinata*. These two closely related sibling species are compared and their specific differences enumerated.

This report, which describes a new northwestern Atlantic cognate species of *A. cristoides* Barnard, 1954, is the first in a series that will deal with members of the benthic amphipod family Ampeliscidae. Material examined for this report came primarily from the Outer Continental Shelf studies of the Minerals Management Service (formerly the Bureau of Land Management) and a study of the benthos of the Mississippi Sound performed by Barry A. Vittor and Associates.

Ampelisca bicarinata, new species, Figures 1, 2, and 3.

Ampelisca cristoides: Barnard 1954b, p. 4, pl. 1, figs. H-J (not *A. cristoides* of Barnard, 1954a).

Material Examined — HOLOTYPE, adult ♀ (16 mm), USNM 210454, 30°01'06"N, 88°20'42"W, Mississippi, November 1980, fine sand, poorly sorted, 24 m; PARATYPES: 2 ♀♀, 1 juvenile, AHF 809, 30°09'89"N, 88°27'63"W, Mississippi, November 1980, medium sand, 24 m, 1 ♀, GCRL 1118, 28°38'N, 97°20'W, DeSoto Canyon, Florida, 27 May 1979, coarse sand, 90 m; 1 ♂, 2 ♀♀, USNM 210455, same collection data; 5 ♀♀, MNHN Am2438, 30°10'N, 87°28'W, Mississippi, November 1980, coarse sand, 24 m.

Other Material — 5 ♀♀, November 1980, 30°09'12"N, 88°38'12"W, fine sand, 13 m; 3 ♀♀, November 1980, 30°06'12"N, 88°22'48"W, fine sand, 12 m; 2 ♀♀, November 1980, 30°04'43"N, 88°12'06"W, fine sand, 12 m; 2 ♀♀, November 1980, 30°01'12"N, 88°17'W, fine sand, 23 m; 4 ♀♀, November 1980, 30°10'48"N, 88°14'W, medium sand, 14 m; 11 ♀♀, November 1980, 30°09'24"N, 88°16'24"W, medium sand, 16 m; 1 ♀, November 1980, 30°09'18"N, 88°11'12"W, medium sand, 16 m; 1 ♀, November 1980, 30°03'18"N, 87°56'W, medium sand, 15 m; 3 ♀♀, November 1980, 30°02'12"N, 87°52'12"W, medium sand, 21 m; 3 ♀♀, January 1976, 29°53'30"N, 88°12'57"W, sand, 32 m; 2 ♀♀, January 1976, 29°43'29"N, 87°43'29"W, medium

sand, 35 m; 1 ♀, July 1976, 29°45'29"N, 87°46'30"W, fine sand, 37 m; 3 ♀♀, July 1976, 29°40'30"N, 87°37'W, medium sand, 36 m; 4 ♀♀, July 1976, 29°54'59"N, 86°04'59"W, coarse sand, 37 m; 2 ♀♀, July 1976, 29°55'59"N, 86°06'28"W, coarse sand, 38 m; 2 ♀♀, January 1976, 29°51'N, 86°06'30"W, medium sand, 41 m; 3 ♀♀, July 1976, 29°46'N, 86°12'30"W, coarse sand, 52 m; 1 ♀, July 1976, 29°24'N, 85°42'02"W, fine sand, 42 m; 1 ♀, July 1976, 29°42'N, 84°11'W, fine sand, 14 m; 1 ♀, July 1976, 29°37'01"N, 84°17'W, fine sand, 19 m; 1 ♀, July 1976, 27°57'N, 83°09'W, fine sand, 19 m; 1 ♀, July 1976, 27°52'30"N, 83°33'59"W, medium sand, 34 m; 1 ♀, January 1980, 27°37'06"N, 82°59'42"W, medium sand, 15 m; 1 ♀, January 1980, 27°38'06"N, 82°54'W, fine sand, 12 m; 1 ♀, January 1980, 27°37'06"N, 82°54'W, sand, 12 m; 3 ♀♀, October 1979, 27°38'06"N, 82°55'06"W, fine sand, 12 m; 1 ♀, October 1979, 27°36'30"N, 82°55'48"W, coarse sand, 12 m; 1 ♀, January 1980, 27°38'48"N, 82°55'48"W, fine sand, 11 m; 1 ♀, January 1980, 27°38'48"N, 82°53'24"W, medium sand, 9 m; 1 ♀, January 1980, 27°36'30"N, 82°53'24"W, medium sand, 12 m; 1 ♀, July 1976, 26°25'N, 82°15'09"W, fine sand, 11 m; 2 ♀♀, July 1976, 26°25'N, 82°58'W, fine sand, 33 m; 1 ♀, July 1981, 26°16'30"N, 82°38'W, fine sand, 26 m; 3 ♀♀, January 1982, 25°47'15"N, 82°25'W, sand, 26 m.

Diagnosis — (Female 14 mm) lower frontal margin of head deeply concave, parallel to upper margin; ratio of length of antenna I peduncular segments 1, 2, and 3 is 100:150:60; antenna I flagella reaching just beyond 4th peduncular segment of antenna II; ratio of antenna II peduncular segments 4 and 5 is 100:70; antenna II about 4/5 length of body; first coxal plate notched anteroventrally; dactyls of pereopods 3 and 4 nearly straight; pereopod 5 posterior lobes of basis gently rounded, bare; pereopod 6 posterior lobe with straight margin, bare; pereopod 7, carpus and merus posterior lobes well-developed, dactyl attenuate, curved forward; pleosomite 3 bicarinate; urosomite 1 with sinuous dorsal margin; uropods 1 and 2 equal, outer ramus of uropod 2 with long terminal spine; uropod 3 rami

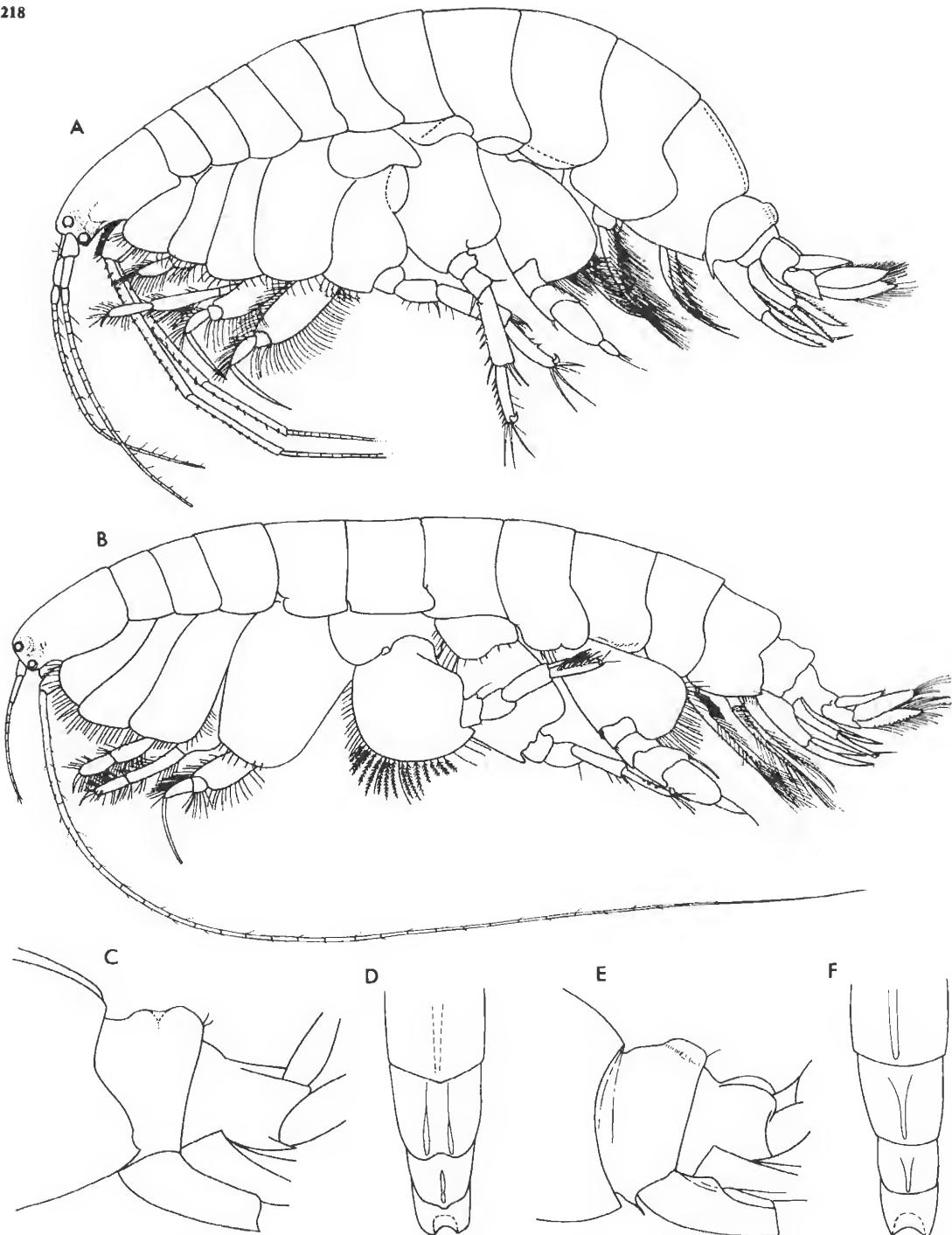


Figure 1. A) Paratype male; B) Paratype female; C) lateral, and D) dorsal view of urosomite of female; E) lateral, and F) dorsal view of urosomite of male.

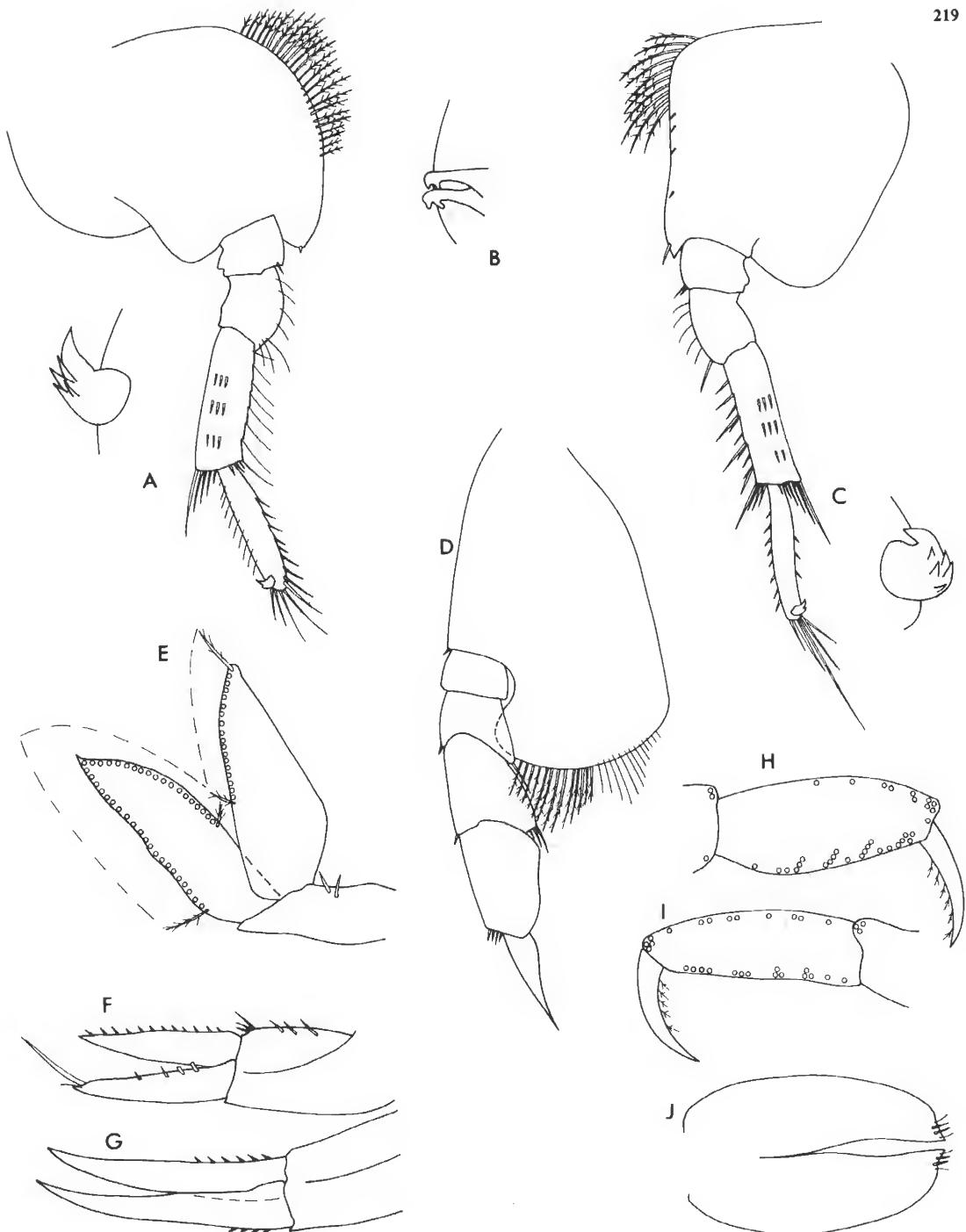


Figure 2. A) Pereopod 5 and detail of dactyl; B) Coupling hooks of male; C) pereopod 6 and detail of dactyl; D) pereopod 7; E) uropod 3; F) uropod 2; G) uropod 1; H) distal segments of pereopods 1, and I) 2; J) telson.

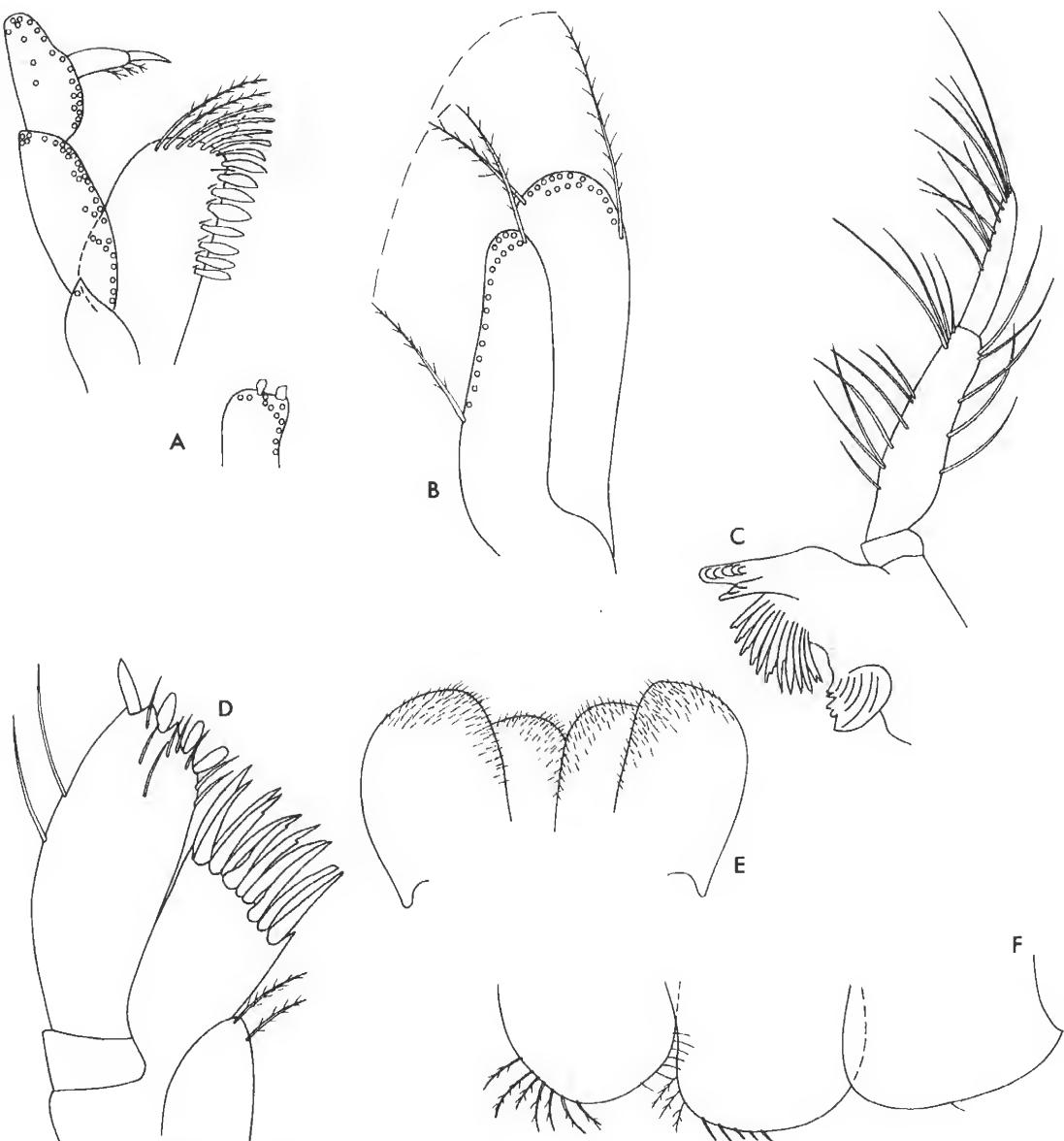


Figure 3. A) Maxilliped; B) Maxilla 2; C) mandible; D) maxilla 1; E) upper lip; F) epimeral plate 1–3.

foliaceous; 3rd epimeral plate slightly sinuous with small posteroventral tooth; dactyls of legs 5 and 6 with numerous accessory teeth; maxilliped, outer plate with about 10 chisel-shaped teeth; inner plate with 2 chisel-shaped teeth and 3 setal spines distally; maxilla 2 with oblique medial margin; gills of female sac-like.

Description — (Female 13.8 mm) — Head with lower margin parallel to upper, lower corneal lens on anteroventral corner, upper corneal lens just about at base of antenna I, head little shorter than first 3 body segments. Antenna I short, about 1/5 length of body, 1st peduncular segment short, stout, with few scattered setae, 2nd and 3rd segments

slimmer with few simple setae, ratio of length of first 3 peduncular segments 100:150:60, flagellum with 9 segments, extending just to tip of 4th peduncular segment of antenna II, flagella with few simple setae at articulations, antenna II about equal to body in length.

Maxilliped: inner plate small, rectangular with apical plumose setae extending along inner margin, 2 chisel-shaped teeth and 1 apical setal spine, 1 subapical facial setal spine; outer plate stout, not reaching end of 2nd article of palp, inner margin with 10 chisel-shaped teeth and 2 plumose setae, chisel-shaped teeth with few accessory setal spines, 2nd article of palp with inner margin lined with 6 setal rows, few setae on outer distal margin, 3rd palp article setose, elongate with dactyl inserted at midlength, broadest basally, dactyl with 2 serrate spines. Maxilla 2; inner plate small, subtriangular, with 2 apical plumose setae, outer plate broad at base with 11 apical spines, all with smaller accessory teeth, palp segment 2 broad distally with few facial simple setae, 1 or 2 simple lateral setae inserted at midlength, 4 apical spines and 3 cusp teeth; basal segments with long cilia. Maxilla 1; inner plate broad basally, narrowing to tip with oblique, slightly concave margin, lateral margin with plumose setal row becoming submarginal distally, apex with long, curved setal spines; outer plate slightly expanded distally with submarginal row of plumose setae, apex with curved setal spines, a few facial plumose setae, basal segments with long cilia. Left mandible: molar heavily sclerotized, spine row with 12 spines, lacinia mobilis well developed with 3 accessory teeth, incisor large with 4 accessory teeth; 2nd palp article elongate, slightly inflated basally, lined with long simple setae, inner margin with few long simple setae submarginally, 3rd article 1/2 length of 2nd with 3 apical simple setae and 5 scattered along margin. Coxa 1 produced anteriorly with large notch at posteroventral angle; coxae 2-4 without notch, normal for genus.

Pereopods 1 and 2 very similar; basis linear, slightly expanded distally with long simple setae on anterior and posterior margins; ischium short with few simple setae; merus short with long simple setae on posterior margin (densest on pereopod 1); carpus of pereopod 1 stout, slightly inflated, length 1.2 times propodus with long, dense, simple setae on posterior margin, carpus of pereopod 2 elongate, thin, 2.5 times length of propodus with long, dense, setae posteriorly and scattered groups of simple setae on anterior margin; propodus of pereopod 1 slightly inflated basally with dense ventral setae, propodus of pereopod 2 slim with dense simple setae ventrally; dactyl of pereopods 1 and 2 short, slightly curved. Pereopods 3 and 4 very similar with 4th slightly more massive; basis elongated, fringed with long plumose setae on margins; carpus short, subquadrate with long plumose setae; propodus long, about 2 times width with plumose dorsal setae on few simple setae on ventral margin; dactyl long, attenuate, nearly straight, length greater than combined propodus and carpus. Pereopod 5; basis expanded, anterior margin evenly rounded with long plumose setae be-

coming submarginal posteriorly, anterior margin slightly overhanging ischium, posterior margin bilobate, lobes gently rounded, bare; ischium short with few simple setae; merus geniculate, anterior and posterior margins with few long simple setae; carpus elongate, rectangular with long simple setae anteriorly, bare posteriorly except for 2 sets of 3 short spines inset, posterior distal margin with several spines varying long to short; propodus elongate, subrectangular with anterior margin lined with setae, terminating with long plumose setae and serrated spines, posterior margin with numerous long serrated spines; dactyl subterminal, main fang with numerous accessory teeth. Pereopod 6: basis expanded, anterior margin angular with long plumose setae at angle and with short simple setae elsewhere, anterior lobe slightly overhanging ischium, posterior lobe with straight margin, bare; ischium short with few simple setae anterodistally; merus short, slightly geniculate with simple setae along anterior margin; carpus elongate, subrectangular with spines (sometimes in groups of 2) along anterior margin and groups of spines posterodistally grading from long to short, longest spine 1/2 length of propodus, 2 subterminal groups of spines; propodus elongate with 2 posterior spines and a series of spines along anterior margin, long terminal spines; dactyl subterminal on propodus with numerous accessory teeth and main fang. Pereopod 7: basis expanded, anterior margin straight with few small spines, posterior margin lobate, extending distally to top of carpus, posterodistal margin oblique, gently rounded, distal margin with long plumose setae and rimmed with minute tubercles; ischium short, subrectangular with 2 anterodistal short spines; merus short with anterior lobe having 4 short spines, posterior lobe 1/2 length of carpus with several long plumose setae; carpus more elongate than merus, anterior lobe well produced with 5 submarginal anterior spines, posterior lobe longer than anterior, blunt apex armed with few short spines and long plumose setae; propodus elongate, expanded proximally, 4 short anterodistal spines and a simple seta posterodistally; dactyl attenuate, anteriorly curved distally; ratio of ischium: merus: carpus: propodus: dactyl is (measured at midlength of segment) 100:82:182:345:235.

Uropod 1 peduncle and rami subequal in length, outer margin of peduncle without spines, inner margin lined with spines, outer ramus devoid of spines, inner ramus with numerous spines along proximal 1/2 of length; uropod 2 extending to end of uropod 1, peduncle little longer than rami, outer margin without spines, inner margin of peduncle lined with spines, outer ramus lined with dorsal spines and with single elongated terminal spine, inner margin lined with spines along entire length; uropod 3 extending 1/2 length beyond telson, outer ramus flattened with plumose setae on distal 1/2 of ventral margin only, inner ramus flattened with plumose setae along ventral margin and on distal 1/2 of dorsal margin; telson deeply cleft with 2 dorsal spines and 4 terminal spines on each lobe.

Epimeral plates 1–3 all rounded anteriorly, plates 1 and 2 with plumose setae on anteroventral margin, plate 1 with simple setae posteriorly, plate 3 with posterior corner produced into weak tooth.

Male — Similar to female in most features except: 1) increased setation of antennae; 2) increased size of plesosome corresponding to increased size of pleopods; 3) a single carina on the plesomites extends up onto the body somites; 4) distal spine of exopod of uropod 2 smaller; 5) dorsal margins of 3rd urosomite produced into collar; 6) carina of urosomite not bicuspat; 7) antenna I flagellum extending almost to end of 5th peduncular segments of antenna II; 8) spines of uropods much more numerous; 9) general body size smaller (10.5 mm); 10) gills of male strongly pleated.

Disposition of Material — The type and/or paratypes have been deposited at the U. S. National Museum of Natural History (USNM), the Allan Hancock Foundation (AHF), the Gulf Coast Research Laboratory (GCRL) and Muséum National d'Histoire Naturelle (Paris) (MNHN). Material examined for this report has been deposited at the USNM.

Variation — Considerable variation has been observed in several features of *Ampelisca bicarinata*. Much of the variation appears to be size-dependent and involves the length of the antennae, shape of the carina of the urosome, the posteroventral process of the third epimeral plate and the relative length of antenna I to the peduncular segments of antenna II. Juveniles of the proposed species often possess an elongate antenna II, which may exceed the length of the body. This variation is common among juvenile ampeliscids where the antennae may be longer than those of the adult. The "normal" condition is where the antennal flagellum is roughly 4/5 the length of the adult animal. The shape of the carina of the urosomite is also a feature which varies from one individual to the next. This variation is also evident in the cognate Pacific species *Ampelisca cristoides*. Barnard (1954b) illustrated some of the variation found in this feature but had no material from the Gulf of Mexico for comparison. In the eastern and northern Gulf populations, the carina is more nearly the saddle-shaped carina, whereas in the lower latitudes the bicuspat nature of the carina becomes more obscured.

The posteroventral margin of the third epimeral plate is often a distinctive character within the genus *Ampelisca* and variation should be noted when found. In most specimens the process is easily discerned but in some specimens it is reduced and nearly absent. Another variation observed in some specimens is the relative length of the flagellum of antenna I to the peduncular segments of antenna II. The condition most often observed is where the tip of the flagellum extends just beyond the articulation of peduncular segments 4 and 5 of antenna II. However, specimens have been examined where the flagellum does not exceed the length of the 4th segment. No relationship was found with either the sex or maturity of the "atypical" specimens.

Range — *Ampelisca bicarinata* has been examined from

the Gulf of Mexico from southeastern Florida northward to the waters off Texas and off Georgia in the Atlantic. The previous records of Barnard (1954b) and Mills (1967) indicate this species ranges into the Caribbean Sea off Colombia and into the temperate North Atlantic. Specimens from the Gulf of Mexico were examined from a bathymetric range of 9–59 m.

Etymology — The specific name is derived from the Latin "bi," two, and "carinus," ridge. It refers to the double crested carina on the third plesomite of the female.

Remarks — *Ampelisca bicarinata* is closely related to *A. cristata* Holmes, 1908, and *A. cristata microdentata* Barnard, 1954. It may be separated from these taxa by the shorter antenna I of the female, the well developed lateral carinae of plesome 3, and 2 rather than 3 chisel-shaped teeth on the terminal margin of the inner plate of the maxilliped and the stronger carina of the urosome.

Ampelisca bicarinata and *Ampelisca cristoides* are very closely related and appear to be recently evolved sibling species. Based on the comparative morphologic evidence presented in Table I and available geological data we suggest that the northeastern Pacific and northwestern Atlantic populations of the ancestral stock of these two species became reproductively isolated during the emergence of the isthmus of Panama some 5 to 23 million years ago (Woodring 1974).

Ecological Notes — In the northern Gulf of Mexico, *Ampelisca bicarinata* is a common member of the benthic polyhaline communities where sand is abundant. Sediment analysis of the occurrence of the proposed species from the area just south of Mississippi Sound has shown the animal is most common in sediments with a very high sand fraction. In stations where sediment data are available, the species was collected from substrata with ranges of 74 to 99% sand. Samples collected from outside the mouth of Tampa Bay were gathered from bottoms of 88 to 99% sand. It appears the species is restricted to regions with very high sand fractions and oceanic salinities.

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TABLE I.
Comparison of selected morphological characters.

	<i>A. bicarinata</i>	<i>A. cristoides</i>
Antenna I peduncular ratio	100:150:80	100:190:80
Antenna I flagellum length	flagellum reaches just beyond articulation of segments 4 and 5 of Antenna II peduncle	flagellum reaches to distal 1/2 of Antenna II peduncular segment 5
Number of flagellar articles	Antenna I: 10 Antenna II: 30	Antenna I: 16 Antenna II: 38
Spines on exopod of uropod 2	6-13	16-22
Terminal spine of uropod 2	greater than 1/2 length of exopod	less than 1/2 length of exopod
Pereopod 2	carpus greater than 1/2 length of propodus	carpus less than 1/2 length of propodus
Pereopod 5	anterodistal lobe of basis well developed	anterodistal lobe of basis poorly developed
Pereopod 7	posterior lobe of merus less than 1/2 length of carpus	posterior lobe of merus greater than 1/2 length of carpus
Urosomite 3	dorsal collar poorly developed	dorsal collar well developed
Carina of urosomite	poorly bicuspat; large	saddle-shaped; massive
Mandible	12 rakers	14 rakers
Maxillipedal inner plate	2 blunt chisel-shaped teeth	2 acuminate chisel-shaped teeth

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DISTRIBUTION OF THE MARSH PERIWINKLE *LITTORINA IRRORATA* (SAY) IN A VIRGINIA SALT MARSH

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ABSTRACT *Littorina irrorata* varies over its geographic range in maximum size, preferred elevations relative to tidal datum planes, and in the type of vegetation it inhabits. On Wallops Island, Virginia, postlarvae of *Littorina irrorata* with shell lengths < 5 mm long live almost exclusively in dead, curled-up leaves of *Spartina alterniflora* at elevations near mean tide level, below elevations occupied by larger conspecifics. Snails longer than 5 mm in length increase in average size with decreasing elevation. This distribution is opposite to that found by Hamilton (1978) in a marsh in Florida. No difference was found in our study area in growth rate of marked snails at two different elevations, so the size-elevation gradient probably is not caused by differences in growth rate. Snails 15 to 19 mm long are more active when exposed to reduced salinities than snails > 21 mm long. The lowest salinities recorded in the marsh occurred at the highest elevations. This salinity effect, together with mortality from known size-selective predators, may account, at least in part, for the seaward increase in mean shell size.

INTRODUCTION

Many species of intertidal gastropods segregate by size on shore. The size segregation pattern exhibited by a species probably reflects size-specific responses to environmental gradients related to elevation and time of tidal inundation and exposure (Edwards 1969, Vermeij 1972). Vermeij (1972) described two types of size distributions among intertidal gastropods. In type-1, shell length increases upshore; this probably results from higher mortality among small individuals at higher elevations caused by physical extremes such as temperature, drying, or salinity extremes. Snails with a type-2 distribution increase in size downshore, probably because of higher mortality among small individuals at lower elevations, resulting from biological interactions such as predation or interspecific competition. The type-1 distribution is most frequent in species occupying high intertidal zones; type-2 is more common at lower intertidal levels.

Littorina irrorata (Say), the salt marsh periwinkle, is found in salt marshes bordering the Atlantic and Gulf coasts of the United States from New York to Texas (Bequaert 1943). *L. irrorata* feeds largely on *Spartina* detritus (Alexander 1976, Stiven and Kuenzler 1979). The snails occupy elevations between mean tide level and mean high water, but part of the population may actively maintain a supralitoral distribution by crawling up stalks of rooted vegetation after being wetted by the incoming tide (Bingham 1972a, Hamilton 1976, Stanhope et al. 1982).

Smalley (1959), working in Georgia, found highest *L. irrorata* densities in short-form *Spartina alterniflora* Loisel; he found few periwinkles in levee and middle-marsh zones. Hamilton (1978) studied *L. irrorata* on the Gulf coast of Florida. He found that snails < 13 mm in length occurred

throughout the *S. alterniflora* zone, but larger snails were found mostly in the upper half of the zone. According to Hamilton's data, *L. irrorata* appears to fit Vermeij's (1972) type-1 distribution, with mean shell size increasing upshore.

The purpose of this study was to determine the distribution limits of *L. irrorata* and the patterns of its size-class segregation with respect to elevation and tidal datum planes in a salt marsh on Wallops Island, Virginia. Tolerances of snails to a range of reduced salinities were determined experimentally for comparison with snail distribution patterns and with salinities measured in the field.

METHODS

The study site is a juvenile sloping foreshore marsh (Redfield 1972) located on Cow Gut Flat at the north end of Wallops Island, near Chincoteague, Virginia (Reidenbaugh and Banta 1980). Drainage at low tide is nearly complete, and freshwater input is limited to rainfall and minor groundwater discharge. No tidal creeks or primary pans are present. Tall and medium vigor *Spartina alterniflora* predominates. *Salicornia* spp. are abundant at some higher elevations; the highest elevations are dominated by saltbush, *Iva frutescens* Linnaeus (Reidenbaugh 1978, Reidenbaugh and Banta 1980). The study site has been named the IBIS (Intensive Biometric Intertidal Survey) Marsh (Reidenbaugh and Banta 1980).

Tidal wrack, consisting primarily of dead stalks of *S. alterniflora*, forms mats which are rafted into the site during extreme high tides (Reidenbaugh and Banta 1980). Vegetation compressed beneath stranded mats is often partially or completely killed. In the most severe cases, bare mud areas form (Figure 1).

Field work was conducted within a 17,000-m² study site marked by wooden stakes placed in a rectangular grid at 10-m² intervals from below mean low water to above mean high water. The elevations of all sampling sites, located in

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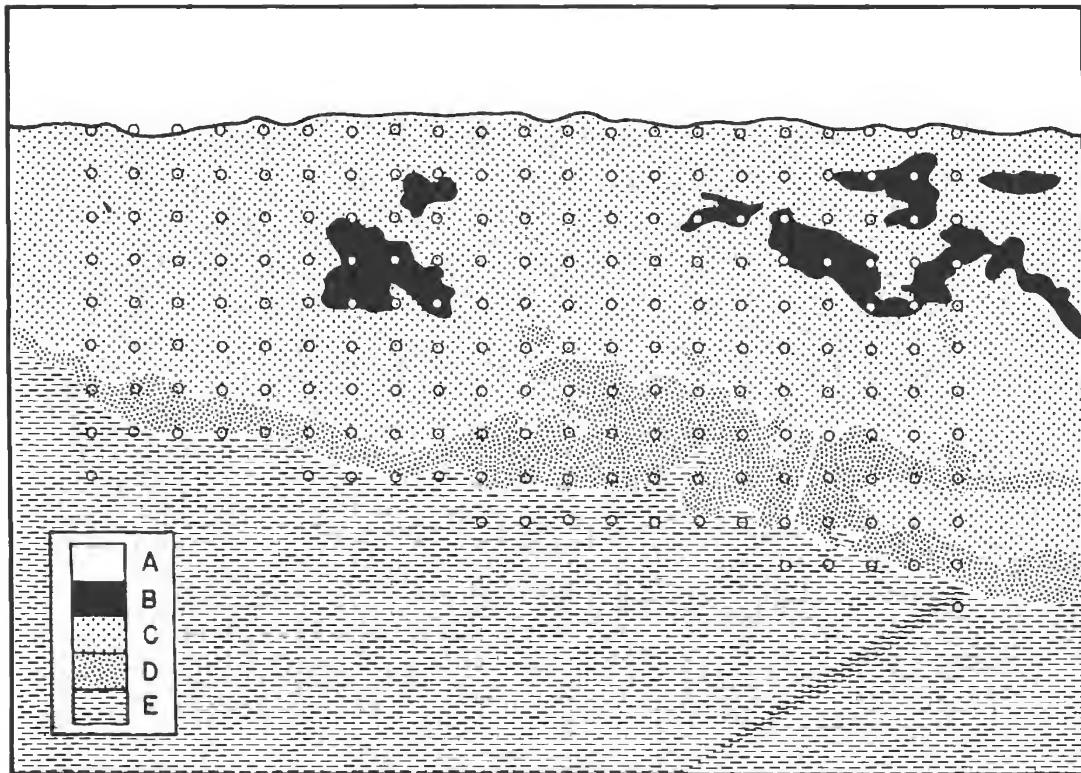


Figure 1. Vegetation map of the IBIS study site made from aerial photographs taken during 1975. Stakes marking sampling locations are represented by circles 10 m apart. Cover types: (A) tidal wrack, (B) bare soil, (C) middle marsh, (D) tall and levee *Spartina alterniflora*, (E) water. Redrawn from Reidenbaugh (1978).

the same relative position 1 m from each stake, were determined by surveying to the nearest stake. Stake elevations were determined relative to a local bench mark; its elevation was in turn determined relative to a U.S. Coast and Geodetic Survey (USGS) bench mark 1 km from the site (Reidenbaugh et al. in press). Tidal datum planes were calculated using estimates from the U.S. National Ocean Survey for Chincoteague, Virginia. The mean tidal range is about 0.8 m. Details are available in Reidenbaugh (1978).

The population density of *L. irrorata* was determined within quadrats at each sampling site three times during the summer of 1975 on 23–25 May, 2–5 July, and 3–10 September. Counts were made in 0.25-m², 0.50-m², or in 1-m² areas, depending on the density and types of vegetation present in each quadrat. The same areas were searched at each site on each sampling date. During two additional censuses made during 23–30 June and 17–30 September, shell length measurements were made with calipers of all periwinkles > 5 mm long in 1-m² quadrats along three of the 20 transects in the sampling grid. Snails < 5.0 mm in length were counted in 0.125-m² parts of each quadrat along three transects of the grid.

To determine growth rates of snails at different elevations, 167 individuals from two quadrats were marked, measured, and released to the same quadrats on 8 August, 1975. The quadrats selected were at elevations of 0.15 and 0.20 in. Marked snails were recaptured and measured 50 days later. To mark the snails, they were dried with paper towels, and a small tag of red fingernail polish was applied. After the polish dried, they were uniquely numbered in black India ink and coated with polyurethane.

About 200 salinity measurements were made on an almost daily basis from May to September using a hand refractometer, calibrated against ten dilutions of standard sea water and read to 0.5 ppt. Salinity readings of tidal water were taken midway between the surface and the bottom. Interstitial salinities were measured by placing a core sample from 2 to 3 cm below the surface into a 50-ml plastic syringe and extruding water through a filter onto a refractometer. Salinity measurements were made from cores taken from six transects sampled between June and September. Additional salinity measurements were made from other sampling locations, such as bare areas and depressions, where topographic and vegetational differences suggested variations in drainage.

The method used to determine salinity tolerance was similar to that used by Arnold (1972). Snails were collected adjacent to the sampling grid in an area where they were most abundant. The snails were divided into two size classes, 15–19 mm and 22–25 mm. Five snails from each size class were placed in a 250-ml Erlenmeyer flask containing sea water dilutions of 0, 5, 8, 10, 15, 20, or 30 ppt made from commercial sea salts (Instant Ocean®) and distilled water. Each flask was stoppered with a 2-hole rubber stopper to keep the snails submerged; the water was aerated using glass tubing extending to the bottom of the flask. Activity of each snail was scored between 11:00 A.M. and 2:00 P.M. daily, and the mean was recorded. All salinities were run simultaneously to eliminate possible systematic variations among snails caused by tidal rhythms. The activity scores used were: 0, dead; 1, inactive, retracted inside the shell, and not attached to the flask; 2, retracted inside the shell and attached to the side of the flask by a mucous holdfast; 3, attached to the side of the flask with the foot extended; 4, actively crawling with the head and foot extended. Snails were considered dead if they did not respond to probing of their foot or operculum within 1 hour after removal from the water.

RESULTS

Distribution of snails less than 5 mm long

The smallest snails, those with a shell length < 5 mm, generally were distributed quite differently from larger snails. The smallest snails were of two types. By far the largest numbers were found inside the curl of dead leaves of *Spartina alterniflora*, just distal to the ligule. They were usually arranged in tandem, like peas in a pod, with as many as 13 in a single leaf. These snails were found in a relatively narrow range of elevations, peaking near 0 m National Geodetic Vertical Datum (NGVD) near mean tide level (MTL). These snails reached very high densities, averaging over 300/m² near 0 m. A much smaller number of snails < 5 mm long, was found at the base of rooted vegetation or on the mud surface high in the marsh from about 0.3 to 0.4 m (about mean high water neap tide, MHWN, to mean high water, MHW) (Figure 2).

Snails greater than 5 mm in length

When periwinkles reach a shell length over about 5 mm, they graze on the marsh floor or attach to the surface of emergent vegetation.

The density-elevation distribution of snails > 5 mm remained fairly constant from June to September (Figure 3). Densities peaked sharply from about halfway between MTL and MHW, with a mean density of 48/m² (Figure 3). The maximum density recorded from a single quadrat was 140/m². About 85% of the population was found between -0.05 and 0.35 m NGVD. Population density decreased sharply above MHWN. Only 2% of the population occurred above

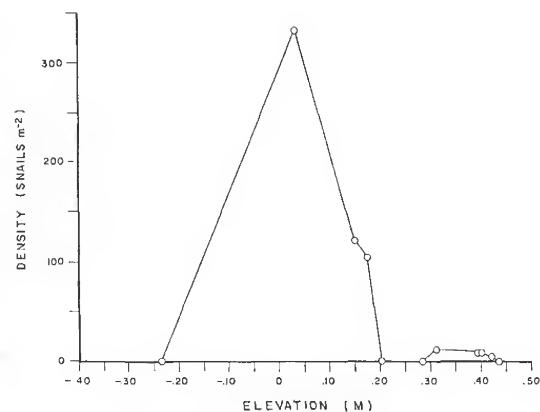


Figure 2. Density distribution of *Littorina irrorata* < 5 mm long plotted against elevation in m NGVD. Zero meters NGVD at this site is very near Mean Sea Level. Data from July 1975. No quadrats were sampled from elevations between -0.23 and 0.03 m.

mean high water spring tide (MHWS), and virtually all of those snails were found beneath tidal wrack; a high proportion of them were dead. Those snails accounted for a slight tail on the distribution curves above MHWS (Figure 3), and probably represent individuals rafted above their normal range by clinging to wrack.

Snails > 5 mm long achieved peak densities in medium growth form of *Spartina alterniflora*, but also were abundant in tall and levee *Spartina* (Reidenbaugh 1978). Few snails were found at any elevation in areas devoid of standing vegetation, or in areas covered by thick mats of *Spartina* wrack. With these exceptions, no coincidence was found between sudden changes in snail density and changes in vegetation type. For example, no snails were found below -0.15 m, even though *Spartina* occurs well below this, to about -0.30 m (Reidenbaugh et al. 1982). Low densities of *L. irrorata* occurred in areas where *Salicornia* spp. were abundant, mixed with *S. alterniflora* (elevations about 0.4 to 0.6 m) (Reidenbaugh 1978). However, *L. irrorata* also occurred at about the same densities at the same elevations in regions where *S. alterniflora* dominated and *Salicornia* was uncommon.

Snail density varied considerably within elevation intervals. Calculation of chi-square, using variance to mean ratios (Elliot 1971), demonstrated that the population is clumped ("contagious", $p < 0.05$) within all but the two elevation intervals about MHWS. These exceptions occurred where the snail population was small and apparently distributed at random.

The total population of snails > 5 mm long declined early in the summer, then increased to a maximum in early fall; there was a 14% increase between May and July and a 23% increase between July and September (Table 1; Figure 3). Relative densities within elevational categories, however,

Table 1.
Density distribution of *Littorina irrorata* >5 mm long.

Elevation interval (m)	Quadrats Sample	May			July			September					
		No. Snails	Mean m ⁻²	Std. Dev.	%	No. Snails	Mean m ⁻²	Std. Dev.	%	No. Snails	Mean m ⁻²	Std. Dev.	%
.700 to .749	3	0	0.0	—	—	0	0.0	—	—	0	0.0	—	—
.650 to .699	3	0	0.0	—	—	0	0.0	—	—	0	0.0	—	—
.600 to .649	7	2	0.3	0.5	0.1	1	0.1	0.4	0.1	2	0.3	0.5	0.1
.550 to .599	3	2	0.7	0.6	0.2	2	0.7	1.2	0.3	3	1.0	0.0	0.3
.500 to .549	12	21	1.8	3.3	0.6	3	0.2	0.8	0.1	35	2.9	4.3	1.0
.450 to .499	10	25	2.5	4.3	0.9	19	1.9	2.5	0.7	22	2.2	2.4	0.7
.400 to .449	20	136	6.8	6.3	2.4	136	6.8	7.4	2.7	183	9.2	7.7	3.1
.350 to .399	13	173	13.3	25.9	4.7	116	8.9	11.7	3.5	158	12.2	13.5	4.1
.300 to .349	14	438	31.3	43.0	11.1	381	27.2	23.6	10.8	430	30.7	32.4	10.3
.250 to .299	15	476	31.7	33.5	11.2	305	20.3	19.1	8.0	457	30.5	28.6	10.2
.200 to .249	25	656	26.2	22.2	9.3	552	22.1	14.1	8.7	747	29.9	25.2	10.0
.150 to .199	12	600	50.0	26.6	17.7	497	41.4	23.0	16.3	634	52.8	22.9	17.7
.100 to .149	7	223	31.9	19.0	11.3	189	27.0	29.6	10.6	160	22.9	20.4	7.7
.050 to .099	8	220	27.5	24.1	9.7	263	32.9	31.6	12.9	259	32.4	32.4	10.8
.000 to .049	6	142	23.7	36.6	8.4	149	24.8	22.2	9.7	151	25.2	21.7	8.4
-.050 to -.001	5	69	13.8	11.3	4.9	138	27.6	19.3	10.8	135	27.0	20.6	9.0
-.100 to -.051	3	52	17.3	18.0	6.1	30	10.0	10.0	3.9	59	19.7	20.0	6.6
-.150 to -.101	3	11	3.7	4.0	1.3	7	2.3	4.0	0.9	0	0.0	—	—
-.200 to -.151	1	0	0.0	—	—	0	0.0	—	—	0	0.0	—	—
-.250 to -.201	4	0	0.0	—	—	0	0.0	—	—	0	0.0	—	—
-.300 to -.251	3	0	0.0	—	—	0	0.0	—	—	0	0.0	—	—
Total	177	3245	282.1		99.9	2788	254.2		99.9	3435	298.9		100.0

changed little and the density distribution remained fairly constant (Table 1). In other words, net changes in relative population density appeared to be relatively independent of elevation. Stiven and Kuenzler (1979) estimated mortality of *L. irrorata* in several experimental pens in North Carolina. They recorded much higher mortalities, up to 90% within a few weeks. However, these results were based on pooled data from experimental cages with sizable artificial alterations in density, experimental changes in initial size-frequency distributions, and variations in the amount of decaying vegetation that was added to each sampling site. Elevations were not measured. No direct comparisons seem possible.

Size-frequency distributions for June and September are shown in Figure 4. The curve for June was weakly bimodal and negatively skewed. Larger snails were most abundant, with a peak at 24 mm shell length; a second peak occurred at a shell length of 19 mm. In September the distribution was similar, but a new peak appeared at 11 mm. The overall population increase (23%) during the interval between samplings was evident, but a decrease in the numbers of snails > 25 mm long suggests some mortality among snails in that size class. Frequency generally increased with size; that is, larger snails were most abundant, suggesting that large snails are relatively long-lived.

The mean length of snails > 5 mm decreased with increasing elevation ($p < 0.01$) (Figure 5). Size-frequency dis-

tributions for snails from each of five elevation intervals are shown in Figure 6. The three peaks seen in Figure 4 are evident, with small, medium, and large snails in some or all of the elevation intervals. Each of the three size classes appear to be distributed differently along the elevation gradient. In June, the smaller snails (5–14 mm) showed peak densities between 0.2 and 0.4 m (near MHWN), but occurred in numbers throughout the marsh. The same was true in September, but peak densities were shifted to lower elevations, between 0.1 and 0.3 m (about midway between MTL and MHWN). Medium-sized snails (15–21 mm) reached peak densities between 0.2 and 0.4 m in both June and September; they dominated the population between 0.3 and 0.4 m (about MHWN to MIIW), but medium-sized snails were almost excluded from lower elevations. The largest snails (> 21 mm) are most abundant between 0.0 and 0.2 m (just above MTL) and are uncommon above 0.3 m (near MHWN). The smallest snails (< 5 mm) peaked sharply at about 0.18 m (Figure 2).

Results of marked snail recapture experiments are summarized in Figure 7. No significant difference in growth rate was observed between the two elevations compared.

Marsh salinity

The results of about 200 measurements of salinity of tidal and interstitial water are shown in Figure 8. The salinity of tidal water varied little, ranging from 30.0 to 32.5 ppt;

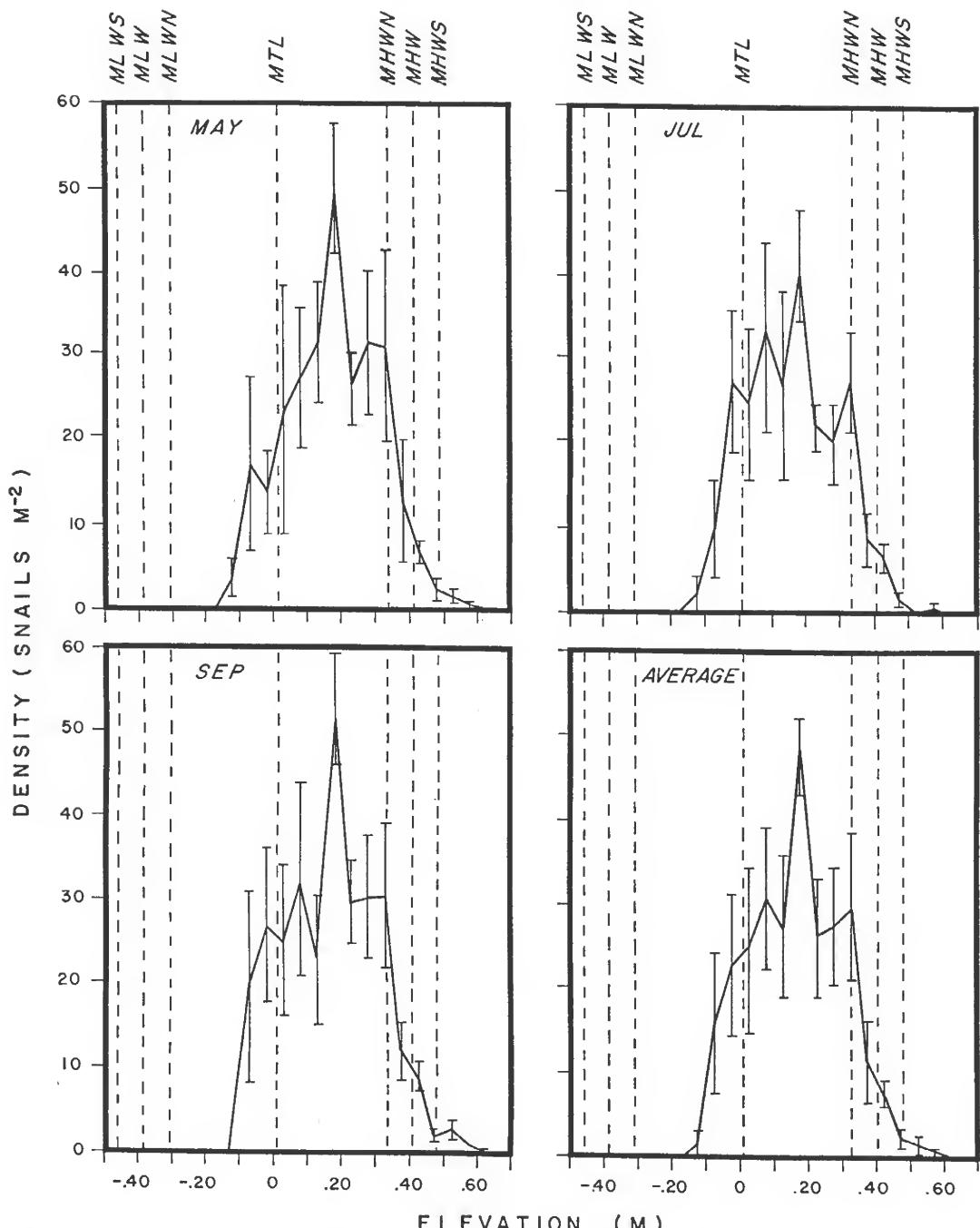


Figure 3. Density of *Littorina irrata* > 5 mm in length plotted against elevation; data from May, June, and September 1975, and averaged for the three sampling periods. The combined counts for each elevation interval were normalized to the number of snails/ m^2 . Vertical bars represent plus and minus one standard deviation. Tidal data are shown as dashed lines.

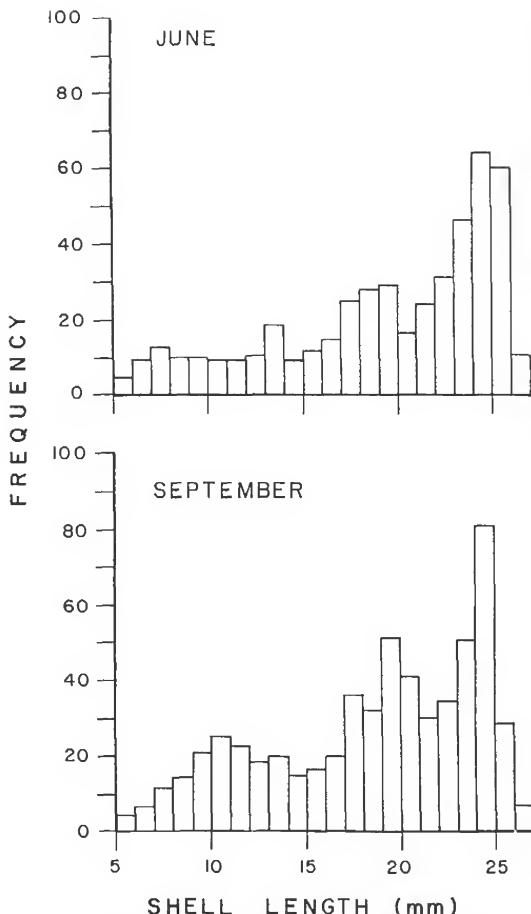


Figure 4. Size density distribution of all *Littorina irrorata* collected during June and September 1975.

the mode was 30.5 ppt. Interstitial salinities were generally less than those measured from tidal water, averaging 27.4 ppt ($n=76$, $SD=6.7$). Interstitial salinity dropped dramatically during rainfall, but returned to near normal levels immediately after inundation by a high tide. Interstitial salinities below about 20 ppt were uncommon in the marsh, and were not recorded at all below MTL, although they probably do occur briefly at low tide during rains. Extremely low salinities of 15 ppt or less were rare, but occurred throughout most of the upper part of the snails' range during or after precipitation (Figure 8).

Tolerance to reduced salinity

Activity levels and percent survival of *L. irrorata* submerged in waters of various salinities are shown in Figure 9. All medium-sized snails (15–19 mm) survived 10 days of

exposure in waters of all salinities tested above that of fresh water, and all survived 5 days or more in fresh water. Larger snails (> 21 mm) were less tolerant; they began to die after 6 days exposure at 5 ppt, and none survived 7 days exposure to fresh water.

Mean activity levels also showed differences between large- and medium-sized snails throughout the salinity range studied (Figures 9 and 10). At all salinities below 30 ppt, activity of large snails was less than that of medium-sized snails.

DISCUSSION

Littorina irrorata appears to vary in maximum size among different marshes. The largest snails reported from the Gulf coast of Florida are 20.5 mm long (Bingham 1972a) and 22 mm (Hamilton 1978). An anonymous reviewer of this manuscript, however, states that he or she "encountered Gulf coast *L. irrorata* to at least 27 mm." Smalley (1959)

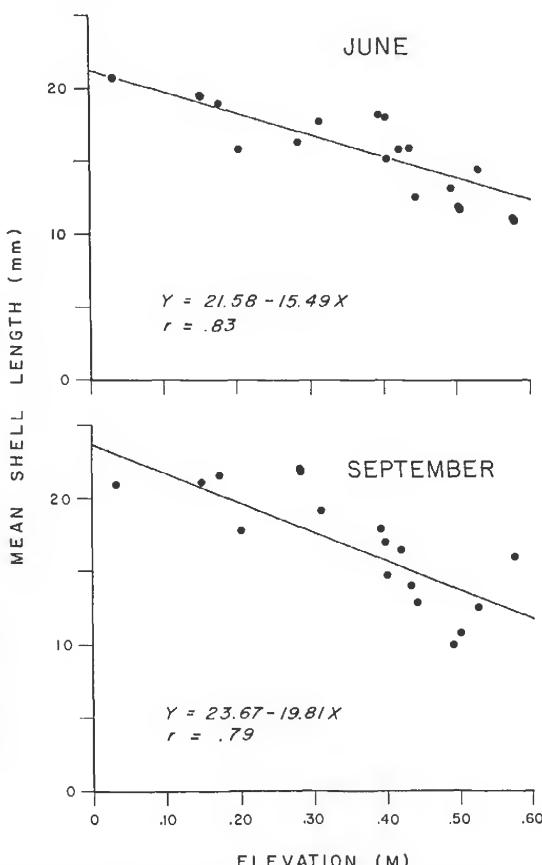


Figure 5. Regression of mean shell length at each sampling site plotted against elevation; data for June and September 1975.

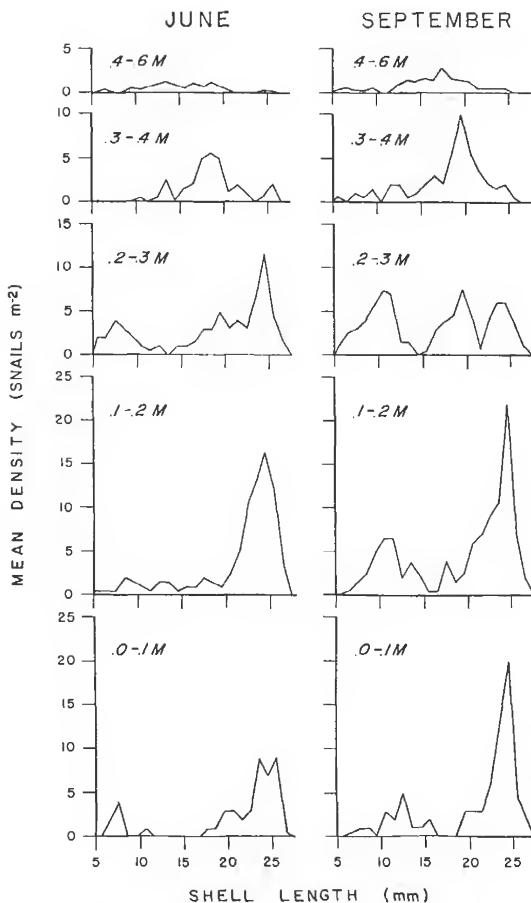


Figure 6. Size-frequency distributions of *Littorina irrorata* for June and September 1975, at five elevation intervals. Frequency was normalized to number of snails/m². Note: graph at top combines data from a 0.2-m interval (0.4–0.6 m). All others are 0.1-m intervals.

found no snails over 21 mm long at Sapelo Island, Georgia. Values calculated from Stiven and Hunter (1976) and Stiven and Kuenzler (1979) using length/width equations from Bingham (1972b) yield maximum lengths near 29 mm from North Carolina. The largest snail found during this study in Virginia was 28 mm long, but individuals up to 29 mm are occasionally encountered in the IBIS Marsh (M. Temkin, Department of Biology, The American University, personal communication).

Mean size of *L. irrorata* is more difficult to compare because of variation in size-frequency distributions with elevation. No other simultaneous measurements of size-frequency and elevation are available, and we know of no previous size-frequency distributions taken on *L. irrorata* collected randomly from all elevations in any marsh. However, the increase in maximum size with increasing latitude

suggests that the same thing may be true of mean size.

Throughout its range, *Littorina irrorata* varies in its distribution relative to tide height and vegetation type. Hamilton (1978) found *L. irrorata* ranging from near MTL to elevations above MHW in marshes dominated by *Spartina alterniflora* and *Juncus roemarianus*. Bingham (1972a) found peak densities in needle rush (*J. roemarianus*) about halfway between MTL and MHW, and indicated that snails > 5 mm long were not common near the marsh-water edge. Smalley (1959) found peak densities of all size classes in short *S. alterniflora* near MHW. He reported that snails > 5 m long were nearly absent near creeks and in levee and middle marsh, although the smallest snails (< 5 mm) were fairly abundant there in leaves of *S. alterniflora*. In the IBIS Marsh, snails occurred in highest densities in medium-height *S. alterniflora* about halfway between MTL and MHW, and were abundant at elevations down to about the middle of the tall *S. alterniflora* zone (Figure 3).

Maximum density of the smallest snails (< 5 mm) occurred near MTL, well below that of any other size class. Most of those snails were distributed in a very narrow tidal range. Smalley (1959) found that the smallest snails were abundant throughout the marsh. He attributed the small numbers of larger snails at low elevations to higher mortality rates among snails at low elevations compared to those at higher elevations. In the IBIS Marsh, members of the next larger size class (5–14 mm) occur throughout the marsh (Figure 6),

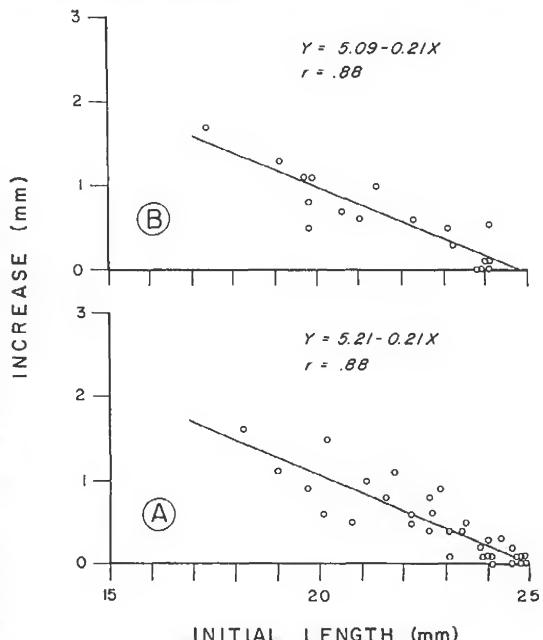


Figure 7. Growth of *Littorina irrorata* during 50 days at elevations 0.15 m (A) and 0.20 m (B).

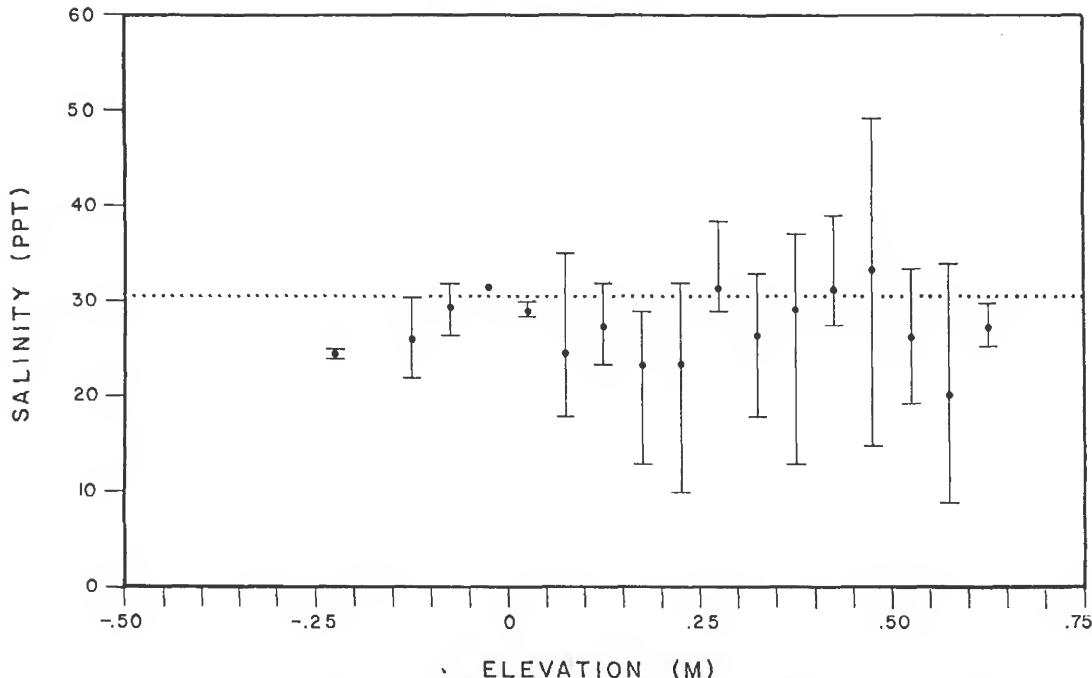


Figure 8. Salinity of water extracted from sediment samples collected within 0.05-m intervals. Average salinities are represented by dots. Vertical bars show the range of salinities measured within each interval. Salinity of tidal water flooding the study site is shown as a dotted line.

although they are most abundant at middle elevations, 0.1 to 0.3 m (Figure 6). These data suggest that the young snail population becomes dispersed in the marsh shortly after they leave dead *S. alterniflora* leaves. The observed distribution pattern of 5–14 mm snails (Figure 6; compare Figure 2) can be explained either by increased mortality at higher elevations or by differential movement of snails upshore to middle elevations (0.1 to 0.3 m). The great difference in numbers of snails between the < 5 mm and the 5–14-mm size classes suggests high mortality among the smallest snails.

The mean length of snails over 5 mm in length decreased with increasing elevation in the IBIS Marsh. *Littorina irrorata*, therefore, seems to have a distribution corresponding to the "type 2" gastropods of Vermeij (1972), in which larger individuals occur lower in the intertidal zone than smaller ones. Vermeij pointed out that such a size distribution is characteristic of species living at lower intertidal levels. He attributed that distribution to predation or other biological interactions which are most intense at lower tide levels. He proposed that the opposite type of distribution, that is, larger snails at higher elevations, arises from physical stresses which are most intense at higher elevations, causing higher mortality among smaller individuals, which are less able to withstand physical stresses.

If snails < 5 mm long were included in the size-elevation calculations, their large numbers and their population peak

at low elevations would indicate that *L. irrorata* fits into Vermeij's "type 1" gastropod category. That is, average size would increase with decreasing elevation, opposite to the distribution of snails more than 5 mm long. On the other hand, the smallest snails occupy a different environment in the marsh than 5–14-mm snails, because the former live in curled-up leaves of *S. alterniflora*, whereas snails > 5 mm live exposed on the marsh surface or on the surface of emergent vegetation. For this reason, combining the smallest snails with those > 5 mm in calculating size-elevation distributions is probably not a meaningful exercise.

Hamilton (1978) found *L. irrorata* distributed opposite to that described here; that is, he reported that mean size increased in an upshore direction. The snail, therefore, apparently responds differently to elevation in different parts of its range.

Stiven and Kuenzler (1979) gave size-frequency data for *L. irrorata* based on 159 individuals. Their data for the Calico Marsh (see their Figure 2) most closely resembles our data for quadrats low in the IBIS Marsh, about -0.1 to +0.1 m; their data from the Causeway Marsh and Tar Landing resemble our size-frequency distributions for elevations higher in the IBIS Marsh (+0.2 to +0.3 m). Furthermore, their density estimates for populations of *L. irrorata* at the Calico Marsh (42/m²) are much higher than at the Causeway (0.8/m²) or Tar Landing (18/m²). (For this example, we

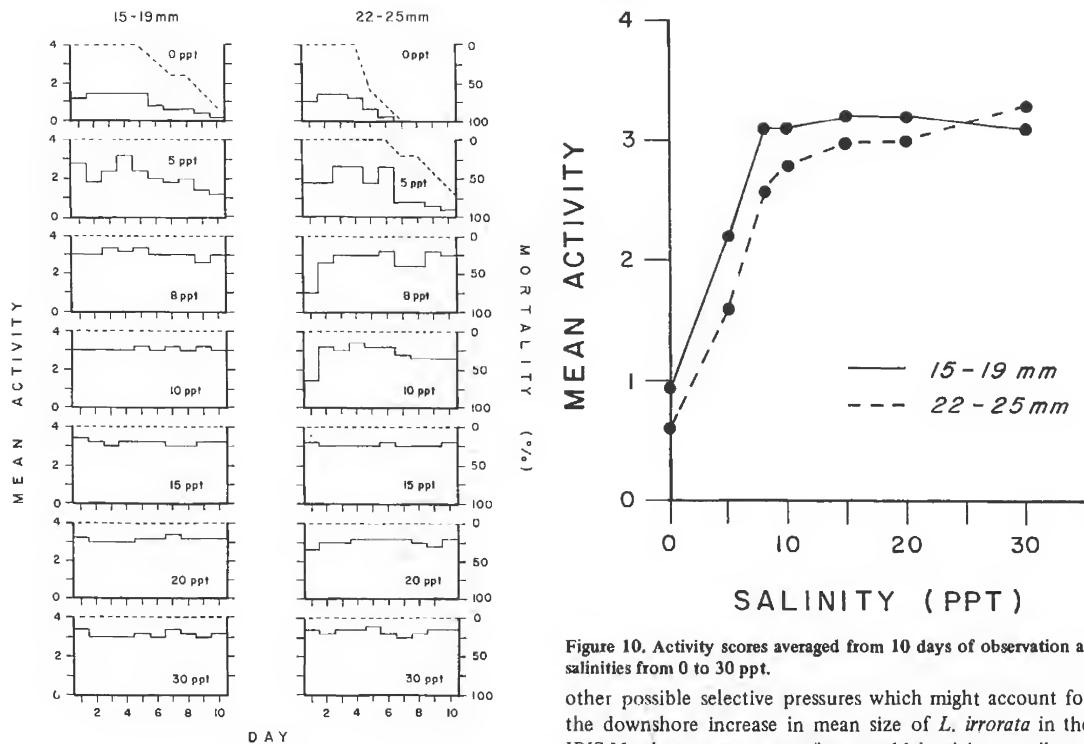


Figure 9. Activity (solid line) and mortality (dashed line) of *Littorina irrorata* in size classes 15–19 mm and 22–25 mm at salinities from 0 to 30 ppt.

arbitrarily used their October data; data for other months are comparable.) Above about 0.15 m in the IBIS Marsh, population densities decreased rapidly with increasing elevation. At least some of the differences among *L. irrorata* populations in the various marshes studied by Stiven and his coworkers may be due to unmeasured differences in elevations among those sites.

At the Calico Marsh, where size-frequency distributions for *L. irrorata* resembled those from the IBIS Marsh from elevations near 0.15 m, Stiven and Kuenzler (1979) speculated that "the relatively low abundance of the smallest size classes...may reflect sparse or sporadic settlement." However, in the IBIS Marsh, settlement of postlarvae of *L. irrorata* is quite heavy (Figure 2). Furthermore, data from summers of 1975, 1976, and 1978 (Banta, unpublished) indicated that settlement was consistently high and that size-frequency distributions remained stable from year to year.

We could measure no difference in growth rates at two different elevations with populations differing markedly in their size-frequency distributions. This would seem to eliminate the possibility that the elevation-dependence of mean size results from differences in growth rate. There are many

Figure 10. Activity scores averaged from 10 days of observation at salinities from 0 to 30 ppt.

other possible selective pressures which might account for the downshore increase in mean size of *L. irrorata* in the IBIS Marsh; we suggest two factors which might contribute: predation and salinity tolerance.

Relatively few predators are known for *Littorina irrorata*. Fish, including the mummichog *Fundulus heteroclitus* (Linnaeus), eat the smallest snails (< 5 mm) (Cherr 1974). Blue crabs *Callinectes sapidus* Rathbun (Hamilton 1976), and apparently clapper rails *Rallus longirostris* Gmelin (Oney 1951) eat snails > 5 mm long. Blue crabs are probably the most abundant and important predators on *L. irrorata* once the snails leave dead *S. alterniflora* leaves. Blue crabs are size-selective predators of *L. irrorata* and cannot eat snails over about 16 mm long (Hamilton 1976, Stanhope et al. 1982). Presumably, predation pressure from blue crabs increases with decreasing elevation because the crabs seldom leave the water. It seems possible, therefore, that blue crab predation may contribute substantially to the downshore increase in average size of *L. irrorata*.

On the other hand, the smaller snails (5–14 mm) are most subject to crab predation, not those over 14 mm (Stanhope et al. 1982). Thus, there is no obvious predation-related reason for the relative scarcity of medium-sized snails (14–21 mm) at low elevations. Perhaps medium-sized snails are crowded out by competition from larger ones, or perhaps there is an unknown predator which enters the marsh with tidal waters and selectively attacks medium-sized snails.

Extreme salinities in the IBIS Marsh did not persist long (seldom for more than one tidal cycle). Because the salinity

of tidal waters varies little within the IBIS Marsh, the probability of a snail experiencing extreme salinities must increase with increasing elevations, and the mean duration of salinity extremes also must increase with elevation. No negative effect was observed on snails exposed to salinities higher than normal, but extremely low salinities (5 ppt) began to kill larger snails (> 21 mm) after 6 days. Fresh water killed large and medium-sized snails (14–21 mm) after 5 days. It seems unlikely that the snails would ever be exposed to those extremely low salinities long enough to kill them. Not only were salinity extremes much shorter lived than 5 days, but snails normally can climb out of the water, whereas our experimental animals were restrained below the surface.

Activity of snails, on the other hand, was depressed at salinities below about 8 ppt. Large snails (> 21 mm) were considerably less active than medium-sized snails (14–21 mm) at any salinity below that of the measured salinity of tidal water in the IBIS Marsh. Assuming that decrease in activity is deleterious, then one would expect to find the observed decrease in mean size with increasing elevation, because the probability of lowered salinity increases with increasing elevation.

SUMMARY AND CONCLUSIONS

1. *Littorina irrorata* varies from marsh to marsh in the type of vegetation with which it is associated, its maximum size, and its size-distribution patterns.

2. At our study site, periwinkles with a shell length < 5 mm were found almost exclusively inside curled-up leaves of *Spartina alterniflora*, and achieved peak densities of more than 300/m² near MTL.

3. Periwinkles > 5 mm in shell length were most abundant halfway between MTL and MHW, with mean peak densities of 48/m².

4. The mean size of snails > 5 mm in length decreased with increasing elevation. Within elevation intervals, the snails displayed a contagious (clumped) distribution.

5. Small snails 5–14 mm long were found predominantly at elevations slightly below MHWN. Medium-sized snails 15–21 mm long dominated the population between MHWN and MHW. Snails > 21 mm predominated from MTL to below MHWN.

6. We could detect no difference in growth rates between

snails living at 0.15 and 0.20 m, even though the same elevation categories showed markedly different size-frequency distributions.

7. Extremes of interstitial salinities were more common at higher elevations than at lower ones. Snails between 15 and 19 mm in length are more active at all salinities below 30 ppt than are snails > 20 mm. Snails 15–19 mm long survived longer when submerged in fresh water and sea water at 5 ppt than did larger snails.

8. The main predator of *L. irrorata* in the IBIS Marsh is probably the blue crab *Cuttlectes sapidus*, which preys selectively on smaller snails. This predation may account in part for the seaward increase in mean size of *L. irrorata*.

9. The observed size-elevation distribution of *L. irrorata* in the IBIS Marsh may have been caused in part by the decrease in average salinity with increasing elevation. Large snails showed a greater decrease in activity with decrease in salinity than did smaller snails, and the frequency of lowered salinities increased upshore.

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A Key to the Porcellanid Crab Zoeae (Crustacea: Decapoda: Anomura) of the North Central Gulf of Mexico and a Comparison of Meristic Characters of Four Species

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A KEY TO THE PORCELLANID CRAB ZOAE (CRUSTACEA: DECAPODA: ANOMURA) OF THE NORTH CENTRAL GULF OF MEXICO AND A COMPARISON OF MERISTIC CHARACTERS OF FOUR SPECIES¹

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ABSTRACT A taxonomic key is provided for the two zoeal stages of five genera and six species of the Porcellanidae (Crustacea: Anomura) from the north central Gulf of Mexico. Measurements, carapace structures, and appendages are compared among zoeal specimens of *Euceramus praelongus* Stimpson, 1860; *Petrolisthes armatus* (Gibbes, 1850); *Polyonyx gibbesi* Haig, 1956; and *Porcellana sigsbeiana* A. Milne-Edwards, 1880. Positive correlations are noted between rostral spine length and carapace length in *E. praelongus* (zoeae I) and *P. sigsbeiana* (zoeae I) and in posterior spine lengths and carapace length in *E. praelongus* (zoeae I) and *P. gibbesi* (zoeae I).

INTRODUCTION

Porcellanid crab zoeae are conspicuous members of the plankton owing to their long rostral and posterior carapace spines. Kelly and Dragovich (1967) reported that porcellanid larvae formed the second most abundant group of zooplankton in Tampa Bay, Florida and accounted for 27.4 percent of the total number of zooplankters. Porcellanid zoeae and adults are major components of the diets of commercially important fish (Jillet 1968, Chesney and Iglesias 1979) and crabs (Gore et al. 1978, Gurriaran 1978). Lopez-Jamárez Martinez (1977) noted the importance of porcellanid zoeae as predators on fish larvae.

The biology of porcellanid crabs is not well known, and information concerning porcellanids from the Gulf of Mexico is especially lacking. The objectives of the present study were to devise a key to porcellanid zoeae of the north central Gulf of Mexico, and compare meristic features of collected zoeae with those of previous findings.

MATERIALS AND METHODS

Zoeae of *Euceramus praelongus* Stimpson, 1860; *Polyonyx gibbesi* Haig, 1956; and *Petrolisthes armatus* (Gibbes, 1850) were removed from plankton samples collected from four stations bordering Mississippi Sound, Mississippi, by personnel of the Fisheries Section of the Gulf Coast Research Laboratory, Ocean Springs, Mississippi. Collections were obtained over a three-year period (October 1973 to September 1976) as part of a fisheries assessment and monitoring project, under the Commercial Fisheries Research and Development Act for the National Marine Fisheries Service. Specific information concerning sample collection

and station locations were previously reported (Maris 1980, Maris and Fish, in preparation). Both zoeal stages of *Porcellana sigsbeiana* A. Milne-Edwards, 1880, were removed from continental shelf collections (Franks et al. 1972).

Individual zoeae were identified to stage of development using telson structures, pleopod development and rostral spine setation employing a binocular stereomicroscope. Appendages were mounted in Turtex CMCP 9AF and CMCP 10, and drawings were made using a drawing attachment.

Measurements were made using a calibrated ocular micrometer. Carapace length was measured from the anterior margin of the eye to the insertion of the posterior carapace spines. Rostral and posterior carapace spine length was measured from the distal tip to carapace attachment. Although carapace spine lengths are not taxonomically significant because of inherent variability in length, dependence on curvature and likelihood of breakage (Gore 1970), rostral and posterior carapace spine lengths were calculated as ratios to carapace length. Carapace length, being more constant and less prone to damage, was expressed as a direct measurement.

Each zoeal stage was treated individually, and easily observed, taxonomically significant structures were noted (rostral and posterior spines, carapace, telson, antenna and maxilliped 2). The term "seta" was used according to the definition of Gonor and Gonor (1973b). Notations for maxilliped setation formulas were presented as in Gore (1968).

Lebour's (1943) key with its modifications and a comparison among described zoeae mainly from laboratory rearings (Table 1) were initially used for species and stage separation. The key constructed includes certain species not collected in the current study but present in the northern Gulf of Mexico. The information for *Megalobrachium sorianum* (Say, 1818) came from Gore (1973b) and that for *Porcellana sayana* (Leach, 1820) from Brooks and Wilson (1881) and Gore (1971c, 1972a).

¹This paper resulted from part of a thesis submitted to the Graduate School, University of Southern Mississippi, Hattiesburg, Mississippi 39401.

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TABLE I.
Comparison of larval characteristics in the Porcellanidae mainly from laboratory rearings.¹

	Porcellana Group				Petrolisthes Group			
	Porcellana	Pisidia	Polyonyx	Euceramus	Petrolisthes	Pachycheles	Megalobrachium	Neopisosoma
Ratio of Mean								
Rostral Spine Length (mm):								
Mean Carapace Length (mm)								
Zoeae I	8.0	4.2–4.4	4.0–7.0	3.9–4.0	1.8–8.5	2.6–6.0	2.5–2.9	7.0
Zoeae II	6.3	3.5–4.2	3.5–6.0	3.2 4.0	1.5–10.0	2.9–5.0	1.7–3.5	7.0
Rostral Spine Armature	covered	covered	covered	only 2 ventral rows	covered	covered	sparsely covered ventrally	covered
Ratio of Mean								
Posterior Spine Lengths (mm):								
Mean Carapace Length (mm)								
Zoeae I	3.0	1.1–1.3	0.7–2.4	1.6–2.0	0.6–3.8	1.3–3.0	0.5–2.0	2.0
Zoeae II	4.5	1.0–1.1	0.4–1.6	1.1–1.3	0.4–3.9	1.2–2.0	0.6–2.0	1.5–2.0
Antenna ²								
Zoeae I	exo>endo exo<ant	exo> endo exo<ant	exo> endo exo=2 x ant	exo>endo	exo>endo ⁴ exo<ant	exo>endo exo with 0–3 fine inner margin setae, 0–1 spines	exo>endo exo with 3–4 lateral spines	exo>endo exo with 3 distal spines
Zoeae II	exo=½ x ant exo<endo	exo = ½ x ant exo< endo	endo>ant exo< endo ³	exo=½ x ant exo<endo	exo<endo	exo<endo	exo<endo	exo<endo
Somites with pleopods	2–5	2–4	2–5	2–5	2–5	2–5	2–5	2–5

¹Porcellana, Gore (1971c, 1972a); Pisidia, Shepherd (1969); Polyonyx, Knight (1966), Gore (1968), Shepherd (1969), Shenoy and Sankolli (1973b); Euceramus, Roberts (1968); Petrolisthes, Greenwood (1965), Gore (1970, 1971b, 1972a, b, c, 1975), Yaqoob (1974, 1977, 1979), Shenoy and Sankolli (1975), Huni (1979); Pachycheles, Knight (1966), MacMillan (1972), Gore (1973a) She-

noy and Sankolli (1973a); Megalobrachium, Gore (1971a, 1972a, 1973b); Neopisosoma, Gore (1977).

²exo – exopodite; endo – endopodite; ant – antennule.

³Polyonyx gibbesi Haig, 1956 zoeae II 2/3 endo=exo.

⁴Petrolisthes galathinus (Bosc, 1802) zoeae I exo=endo.

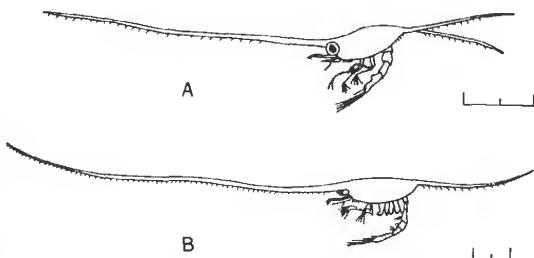


Figure 1. Representative whole specimens of porcellanid zoeae, using *Euceramus praelongus* as the example. A, zoeae I; B, zoeae II. Scale lines equal 0.5 mm.

The measurement data were normally distributed, so parametric statistical tests were used for data analysis. A Pearson correlation (Zar 1974) was used to determine whether a linear relationship existed between rostral spine length and carapace length; or posterior spine lengths and carapace length, for any zoeal stage. A one-tailed t-test (Zar 1974) was employed to decide whether present measurements differed significantly from previous measurements.

Identified collections of all species and stages were deposited in the Museum of the Gulf Coast Research Laboratory (GCRL 1098–1105) and Invertebrate Zoology Collection, Department of Biology, University of Southern Mississippi.

RESULTS

General External Features of Porcellanid Larvae

Porcellanid crab zoeae are characterized by very long, tapering rostral and posterior carapace spines (Figure 1). The single rostral spine is usually not flattened, and can be

from about two to eight times the carapace length. The two posterior spines are about one-half to four times the carapace length. The carapace is smooth and, in the genera considered herein, has no serrated edges. A triangular telson is present with several processes on the spatulate posterior margin. The outer pair of processes are short, smooth spines;

the second are reduced to fine setae as is typical in the Anomura; and the remainder are long, setose spines.

The antennal scale is reduced to an elongate spine. First and second pairs of maxillipeds are functional, but the third is not. Pereiopods, if present, are small and nonfunctional, although enlarging in later zoal development. Five or six abdominal somites are present, but there are usually no

uropods. Three to four pairs of pleopods are present in later stages, and the telson somite is without pleopods. All described species have two zoeal stages except for *Petrocheles spinosus* Miers, 1876, of New Zealand. Wear (1965) found that this species has five zoeal stages and exhibited several other galatheid features. *Petrocheles spinosus* thus appears to exhibit a link between the Porcellanidae and Galatheidae.

KEY TO PORCELLANID CRAB ZOAE OF THE NORTH CENTRAL GULF OF MEXICO

(For comparison of features in key, see Figures 2-7)

1. Pleopods absent or present only as primordia; 5 pairs of plumose setae on telson; carapace length generally less than 1.5 mm; eyes sessile *Zoeae I-2*.
Pleopods present and well-developed; 6 pairs of plumose setae on telson or 5 pairs and a median spine; carapace length generally greater than 1.5 mm; eyes mobile *Zoeae II-7*.
2. Fifth pair of long plumose setae off central prominence of telson; latter may have 2 fine hairs medially; telson length 1.5 times width *Porcellana* group-3.
Fifth pair of long plumose setae on central prominence of telson; hairs on latter usually absent; telson length about equals width *Petrolisthes* group-6.
3. Three to 5 marginal spinules present on carapace just anterior to base of posterior spines; rostral spine with armature reduced to 2 ventral rows of anteriorly directed spinules *Euceramus praelongus*.
Marginal carapace spines lacking or greatly reduced; rostral spine completely covered with setae 4.
4. Length of posterior spines approximately 2 times or less carapace length; antennal exopodite length twice endopodite length; posterior carapace margin with 2 small spinules *Polyonyx gibbesi*.
Length of posterior spines approximately 3 or more times carapace length; antennal exopodite length less than twice endopodite length; posterior carapace margin lacking spinules *Porcellana* spp.-5.
5. Posterior carapace spines widely separated and divergent posteriorly; 1st and 2nd maxillipeds with distinct hook-like spine on basipodite; dorsal hump present on carapace *Porcellana sigsbeiana*.
Posterior carapace spines not widely separated and typically parallel posteriorly; 1st and 2nd maxillipeds without hook-like spine on basipodite; dorsal carapace hump lacking *Porcellana sayana*.
6. Rostral spine distinctly upswept or sigmoid; posterior carapace spines armed ventrally with 2 or 3 large spines *Megalobrachium soriatum*.
Rostral spine straight; posterior carapace spines armed ventrally with numerous small spinules *Petrolisthes armatus*.
7. A 6th pair of long plumose setae added to central prominence of telson; mandibles without palps *Porcellana* group-8.
A single median spine added to telson prominence; mandibles with palps *Petrolisthes* group-11.
8. Three to 5 marginal spinules present on posterior carapace; rostral spine with 2 ventral rows of setae *Euceramus praelongus*.
Marginal carapace spines lacking or greatly reduced; rostral spine completely covered with setae 9.
9. Length of posterior spines less than 2.5 times carapace length; antennal exopodite length about 2/3 endopodite length; 3rd endopodal segment of 2nd maxilliped swollen, twice as long as other segments *Polyonyx gibbesi*.
Length of posterior spines greater than 2.5 times carapace length; antennal exopodite length about 1/2 endopodite length; 3rd endopodal segment of 2nd maxilliped not swollen, about same size as other segments *Porcellana* spp.-10.

10. Posterior carapace spine attachments widely separated and divergent posteriorly; 1st and 2nd maxillipeds with distinct hook-like spine on basipodite; dorsal hump present on carapace *Porcellana sigsbeiana*.
 Posterior carapace spine attachments not widely separated and typically parallel posteriorly; 1st and 2nd maxillipeds without hook-like spine on basipodite; dorsal carapace hump lacking *Porcellana sayana*.

11. Rostral spine distinctly upswept or sigmoid; posterior carapace spines armed ventrally with 1 small spine (rarely 2) ..
 *Megalobrachium soriatum*.
 Rostral spine straight; posterior carapace spines armed ventrally with numerous small spinules. *Petrolisthes armatus*.

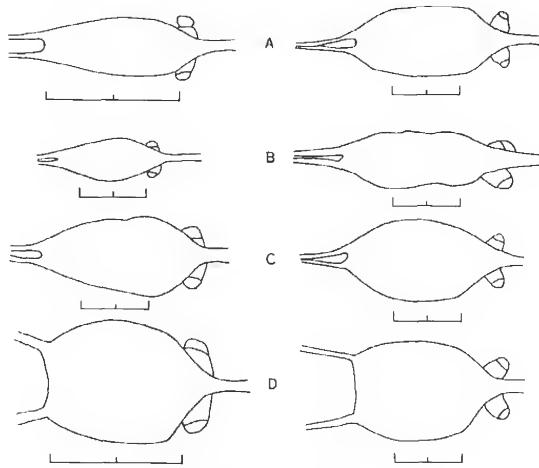


Figure 2. Dorsal region of carapace. Left column, zoeae I; right column, zoeae II. A, *Euceramus praelongus*; B, *Petrolisthes armatus*; C, *Polyonyx gibbesi*; D, *Porcellana sgsbeiana*. Scale lines equal 0.5 mm.

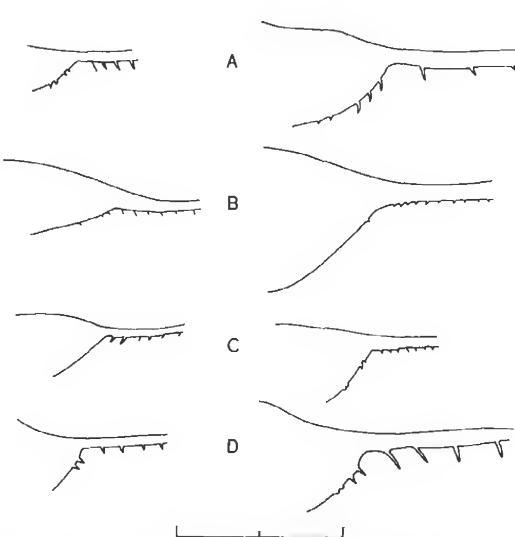


Figure 4. Posterior region of carapace and posterior spines. Left column, zoeae I; right column, zoeae II. A, *Euceramus praelongus*; B, *Petrolisthes armatus*; C, *Polyonyx gibbesi*; D, *Porcellana sgsbeiana*. Scale lines equal 0.5 mm.

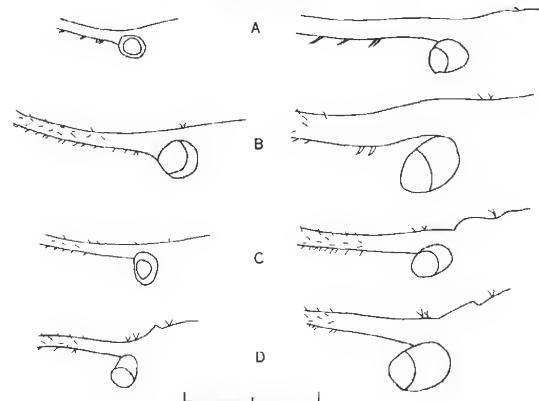


Figure 3. Anterior region of carapace and rostral spine. Left column, zoeae I; right column, zoeae II. A, *Euceramus praelongus*; B, *Petrolisthes armatus*; C, *Polyonyx gibbesi*; D, *Porcellana sgsbeiana*. Scale lines equal 0.5 mm.

DISCUSSION

Gurney (1938) first noticed differences in telson structures between zoeae of *Porcellana* and *Petrolisthes*. Lebour

(1943) devised a general classification of porcellanid zoeae according to telson structures.

Greenwood (1965) included *Pisidia* in Lebour's *Porcellana* group, and noted that *Petrolisthes novaezelandiae* Filhol, 1885, and *P. elongatus* (H. Milne-Edwards, 1837) were exceptions to the proposed groupings. These two species exhibit telson structures, among other features, that do not correspond to Lebour's classification system. Knight (1966) added *Polyonyx* to the *Porcellana* group, *Pachycheles* to the *Petrolisthes* group, and mentioned a relationship between telson length/width ratio. Roberts (1968) placed *Euceramus* in the *Porcellana* group, and Gore (1971a) included *Megalobrachium* in the *Petrolisthes* group. Gore (1971a) stated that *Minyocerus* was possibly in the *Porcellana* group, and later indicated that *Clastotoechus* possibly belonged to the *Petrolisthes* group (Gore 1977). *Neopiso-soma* was placed in the *Petrolisthes* group by Gore (1977).

Wear (1966) created a third group, for *Petrocheles*, Gore (1972a, c) formed a fourth group, the *Petrolisthes platymerus* group, containing *P. platymerus* Haig, 1960, and

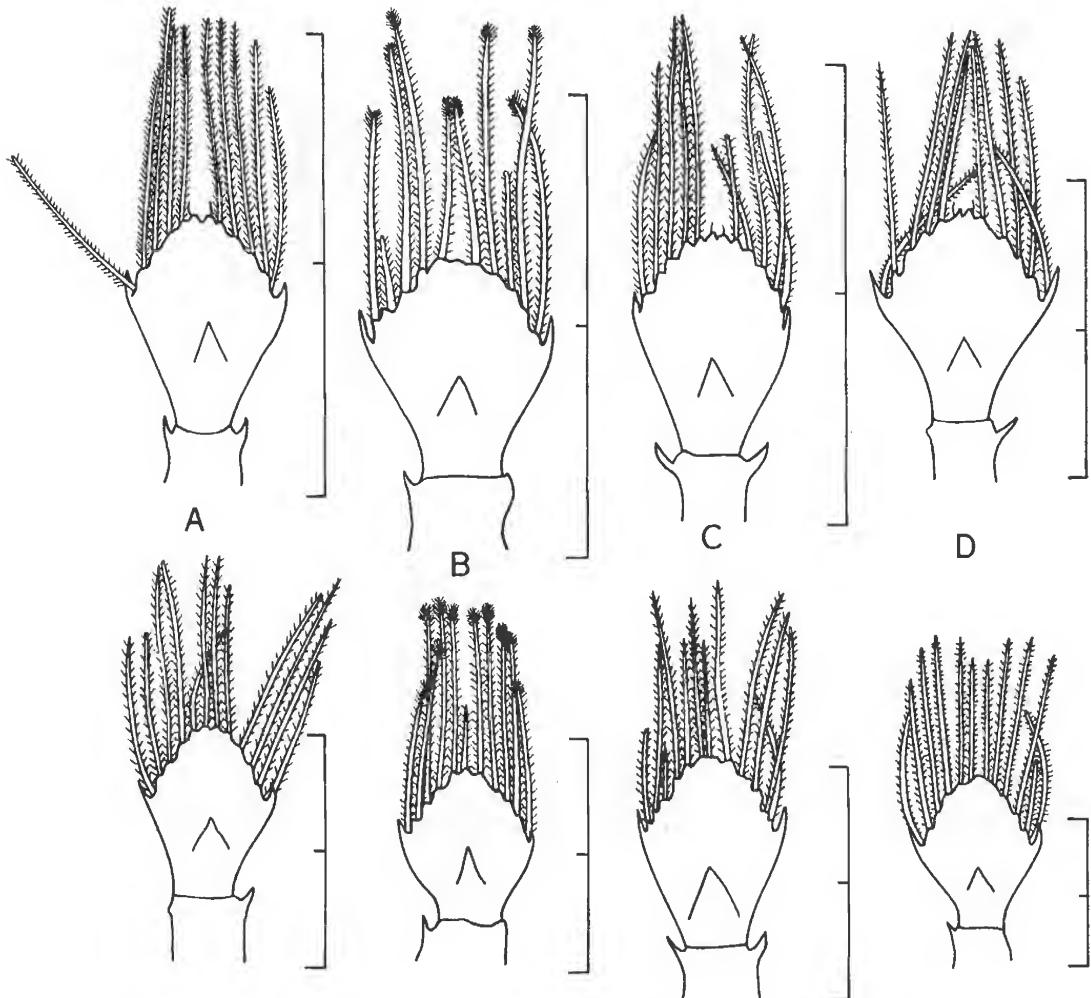


Figure 5. Telson structures. Top row, zoeae I; bottom row, zoeae II. A, *Euceramus praelongus*; B, *Petrolisthes armatus*; C, *Polyonyx gibbesi*; D, *Porcellana sgsbeiana*. Scale lines equal 0.5 mm. Note: certain setae were broken on specimens used in drawings.

tentatively *P. elongatus*. The only other exception to Lebour's classification remains *P. novaezealandiae*.

Larval measurements among four species were compared in Table 2. *Petrolisthes armatus* had the longest carapace lengths for both zoeae I and II, while *Polyonyx gibbesi* had the shortest carapace lengths. *Porcellana sgsbeiana* and *P. armatus* showed the largest and smallest carapace spine lengths (rostral and posterior)/carapace length ratios, respectively. Positive correlations between rostral spine length and carapace length were noted for *Euceramus praelongus* (zoeae I) and *P. sgsbeiana* (zoeae I); posterior spine lengths and carapace length for *E. praelongus* (zoeae I) and *P. gibbesi* (zoeae I).

Zoeae from the present study (planktonic) were compared with zoeae obtained from laboratory rearings, using a one-tailed t-test (Table 3). Measurements on zoeae from the field collections were often slightly larger than those from the laboratory-reared specimens, a fact noted by other authors. All field measurements (except one) differed significantly from ones obtained in the laboratory. Le Roux (1966) found larvae of *Pisidia longicornis* (Linnaeus, 1777) from natural environments larger than those reared in the laboratory. Gore (1968) noted similar size discrepancies in larvae of *P. gibbesi*; specimens from natural environments usually had the longest carapace and rostral spines. Improved conditions in the natural environment, as compared to

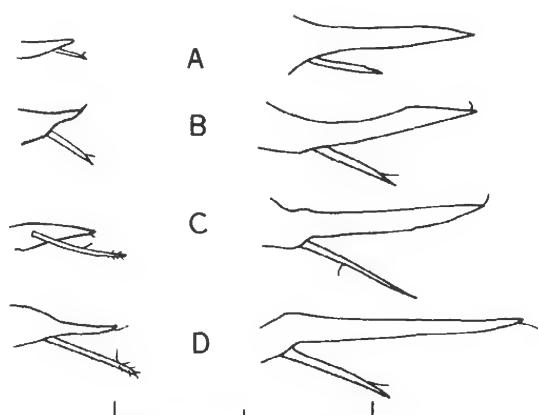


Figure 6. Antenna. Left column, zoeae I; right column, zoeae II. A, *Euceramus praelongus*; B, *Petrolisthes armatus*; C, *Polyonyx gibbesi*; D, *Porcellana sigsbeiana*. Scale lines equal 0.5 mm.

laboratory conditions, may account in part for the observed size differences. Food availability, temperature fluctuations, diel light, and essential chemical concentrations in the water

are but a few of the possible factors which may influence size.

Rostral spines are completely covered with setae in all species and stages except *E. praelongus*, which has only two ventral rows of spinules. Posterior carapacial spines in all species and stages are similar, with two posterior spines, each with a single row of spinules (Figures 3-4). Carapace length exceeds width and posterior spine attachments are not widely separated except in *P. sigsbeiana* which has a nearly rectangular carapace and widely separated posterior spine attachments (Figure 2).

The anterior dorsal region of the carapace is devoid of setation in zoeae I of *E. praelongus*, and a single seta is found in zoeae II of *E. praelongus* (Figure 3). A single pair of setae occurs in *P. armatus* (zoeae I) and two pairs are found in *P. armatus* (zoeae II) and *P. gibbesi* (zoeae I). Three pairs of setae occur in *P. gibbesi* (zoeae II) and *P. sigsbeiana* (zoeae I and II). Roberts (1968) did not mention carapace setation for *E. praelongus*. Gore (1970) found three pairs of dorsal carapace setae in zoeae I and II of *P. armatus*. Gore (1968) stated that *P. gibbesi* (zoeae I) had three pairs of setae. Zoeae II of *P. gibbesi* and both stages of *P. sigsbeiana* have dorsal carapace setation similar to previous studies. Gore (1968)

TABLE 2.

Comparison of Porcellanid Zoeal Measurements (Values in parentheses are means \pm standard deviation); r = Pearson Correlation Coefficient; p = Significance Level; N.S. = not significant ($p < 0.05$).

	<i>Euceramus praelongus</i>	<i>Petrolisthes armatus</i>	<i>Polyonyx gibbesi</i>	<i>Porcellana sigsbeiana</i>
Zoeae I				
Carapace Length (mm)	0.84-1.06 (0.95 \pm 0.06)	1.30-1.36 (1.34 \pm 0.03)	1.00-1.26 (1.15 \pm 0.07)	0.84-0.96 (0.92 \pm 0.05)
Rostral Spine Length/Carapace Length	4.25-5.02 (4.59 \pm 0.25)	4.23-4.42 (4.31 \pm 0.08)	5.04-7.61 (6.16 \pm 0.53)	9.13-9.76 (9.42 \pm 0.26)
	r = +0.6343 p = 0.001	r = +0.7253 N.S.	r = +0.3801 N.S.	r = +0.9663 p = 0.034
Posterior Spine Lengths/Carapace Length	1.60-2.07 (1.83 \pm 0.12)	1.19-1.36 (1.26 \pm 0.07)	1.44-2.04 (1.64 \pm 0.15)	3.04-3.48 (3.33 \pm 0.20)
	r = +0.6082 p = 0.001	r = +0.2353 N.S.	r = +0.5394 p = 0.005	r = +0.4036 N.S.
Sample Size	25	4	25	4
Zoeae II				
Carapace Length (mm)	1.54-1.94 (1.75 \pm 0.11)	1.92-2.28 (2.12 \pm 0.11)	1.54-1.90 (1.74 \pm 0.11)	1.78-1.98 (1.90 \pm 0.06)
Rostral Spine Length/Carapace Length	4.44-6.25 (5.39 \pm 0.52)	4.33-6.21 (5.32 \pm 0.45)	5.96-9.06 (7.45 \pm 0.83)	8.24-10.66 (9.27 \pm 0.58)
	r = -0.1100 N.S.	r = +0.2384 N.S.	r = +0.1779 N.S.	r = +0.1243 N.S.
Posterior Spine Lengths/Carapace Length	1.44-2.00 (1.67 \pm 0.17)	1.17-1.88 (1.62 \pm 0.17)	1.38-2.23 (1.79 \pm 0.26)	2.50-3.23 (2.97 \pm 0.14)
	r = -0.0902 N.S.	r = +0.2620 N.S.	r = +0.0024 N.S.	r = +0.3955 N.S.
Sample Size (n)	25	25	25	25

KEY TO PORCELLANID CRAB ZOAE

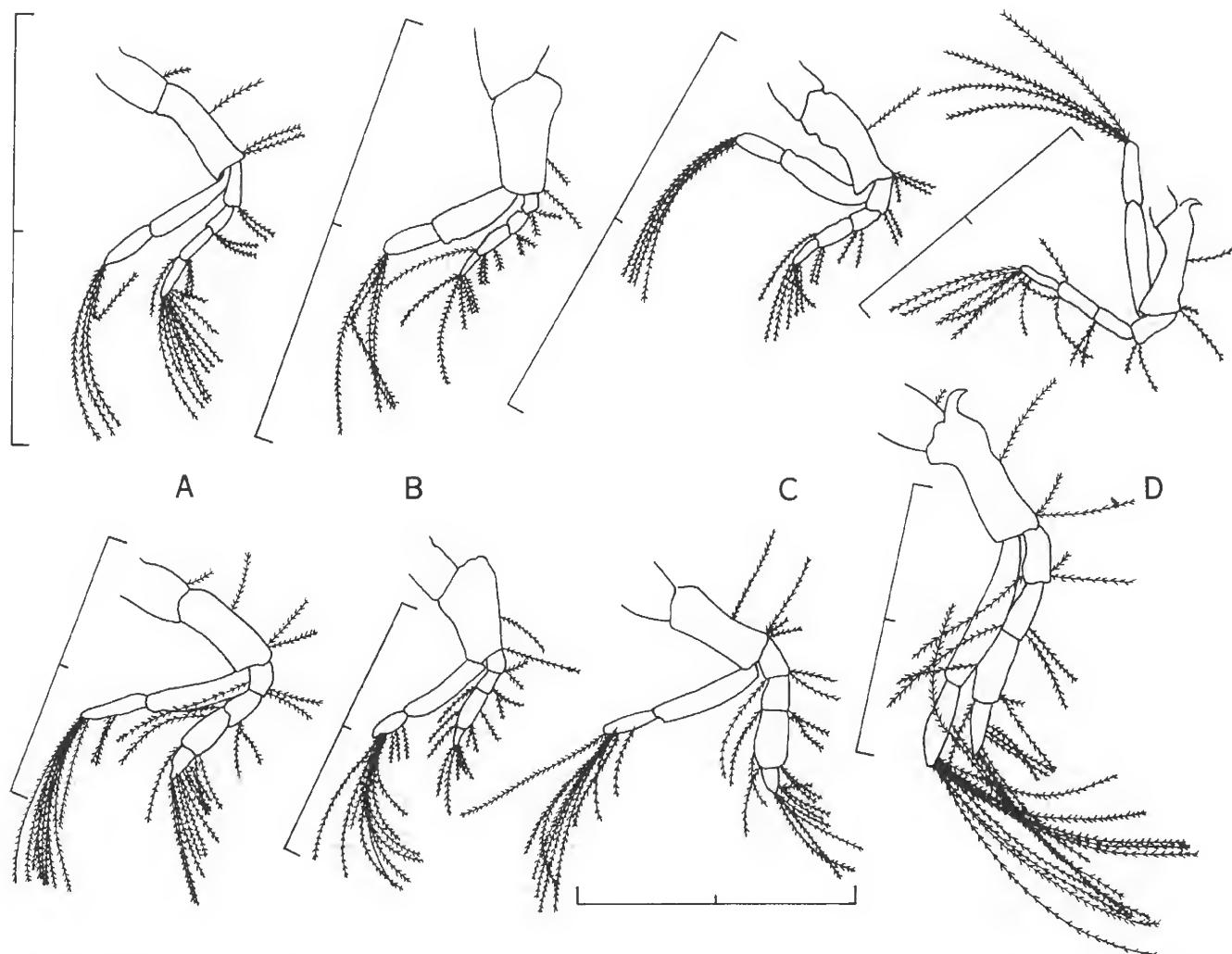


Figure 7. Maxilliped 2. Top row, zoeae I; bottom row, zoeae II. A, *Euceramus praelongus*; B, *Petrolisthes armatus*; C, *Polyonyx gibbesi*; D, *Porcellana sigsbeiana*. Scale lines equal 0.5 mm.

TABLE 3.

Comparisons of Porcellanid Zœal Measurements Obtained from the Present Study and Previous Studies; values are means \pm standard deviation (in present study); significance level (p) indicates results of a one-tailed t-test; n = sample size; N.S. = not significant ($p > 0.05$).

Species	Measurement	Present Study	Previous Studies	Significant Level
<i>Euceramus praelongus</i>			(Roberts 1968)	
zœae I (n = 25)	Carapace Length (mm)	0.95 \pm 0.06	1.02	(p < 0.005)
	Rostral Spine Length/Carapace Length	4.59 \pm 0.25	4.17	(p < 0.005)
	Posterior Spine Lengths/Carapace Length	1.83 \pm 0.12	1.78	(p < 0.05)
zœae II (n = 25)	Carapace Length (mm)	1.75 \pm 0.11	1.80	(p < 0.025)
	Rostral Spine Length/Carapace Length	5.39 \pm 0.52	3.68	(p < 0.0005)
	Posterior Spine Lengths/Carapace Length	1.67 \pm 0.17	1.07	(p < 0.0005)
<i>Petrolisthes armatus</i>			(Gore 1970)	
zœae I (n = 4)	Carapace Length (mm)	1.34 \pm 0.03	1.6	(p < 0.0005)
	Rostral Spine Length/Carapace Length	4.31 \pm 0.08	up to 4	(p < 0.0005)
	Posterior Spine Lengths/Carapace Length	1.26 \pm 0.07	about 1	(p < 0.005)
zœae II (n = 25)	Carapace Length (mm)	2.12 \pm 0.11	2.0	(p < 0.0005)
	Rostral Spine Length/Carapace Length	5.32 \pm 0.45	up to 5	(p < 0.001)
	Posterior Spine Lengths/Carapace Length	1.62 \pm 0.17	about 1	(p < 0.0005)
<i>Polyonyx gibbesi</i>			(Gore 1968)	
zœae I (n = 25)	Carapace Length (mm)	1.15 \pm 0.07	1.2	(p < 0.001)
	Rostral Spine Length/Carapace Length	6.16 \pm 0.53	up to 7	(p < 0.0005)
	Posterior Spine Lengths/Carapace Length	1.64 \pm 0.15	1.4-1.8	N.S.
zœae II (n = 25)	Carapace Length (mm)	1.74 \pm 0.11	1.7	(p < 0.05)
	Rostral Spine Length/Carapace Length	7.45 \pm 0.83	about 6	(p < 0.0005)
	Posterior Spine Lengths/Carapace Length	1.79 \pm 0.26	up to 1.6	(p < 0.001)
<i>Porcellana sigsbeiana</i>			(Gore 1971c)	
zœae I (n = 4)	Carapace Length (mm)	0.92 \pm 0.05	1.12	(p < 0.0005)
	Rostral Spine Length/Carapace Length	9.42 \pm 0.26	up to 8	(p < 0.0005)
	Posterior Spine Lengths/Carapace Length	3.33 \pm 0.20	about 3	(p < 0.0025)
zœae II (n = 25)	Carapace Length (mm)	1.90 \pm 0.06	1.93	(p < 0.01)
	Rostral Spine Length/Carapace Length	9.27 \pm 0.58	up to 6.3	(p < 0.0005)
	Posterior Spine Lengths/Carapace Length	2.97 \pm 0.14	up to 4.5	(p < 0.0005)

mentioned that carapace setation was possibly taxonomically important, but with further examination decided that carapace setation was unreliable for species identification (Gore 1971a).

Zœae of *E. praelongus*, *P. gibbesi*, and *P. sigsbeiana*, from the present study, exhibited telson characteristics of Lebour's (1943) *Porcellana* group, and *P. armatus* showed *Petrolisthes* group features (Figure 5). These findings verify previous reports and show the continued usefulness of Lebour's key.

Antennal exopodites are slightly longer than endopodites in zœae I of *E. praelongus* and *P. sigsbeiana* (Figure 6). Exopodite length is twice endopodite length in *P. armatus* and *P. gibbesi*. Endopodite length exceeds exopodite length for all species in zœae II. No setation is present in zœae II of *E. praelongus* and zœae I of *E. praelongus* have a single

seta on the exopodite. Zœae I of *P. armatus* have a single antennal endopodite seta and a pair of exopodite setae. All other species and stages studied have a single endopodite and exopodite seta.

Table 4 compares maxilliped 2 setation for zœae from present and previous studies with many differences noted in setation formulas (Figure 7). Gonor and Gonor (1973a) found, in a study of four porcellanid species, that setation of larval appendages (maxillæ and maxillipeds) varied considerably between individuals of the same species and stage. Their conclusion was that setation formulas alone are not reliable enough to characterize species or genera or to indicate relationships, at least among their four examined species. Thus, setation differences between zœae from the present study and other studies are probably not taxonomically significant.

TABLE 4.

Comparison of meristic variation of Maxilliped 2 setation; standard formula notation is according to Gore (1968).

Species	Segment	Present Study	Previous Studies	Species	Segment	Present Study	Previous Studies
<i>Euceramus praelongus</i>			(Roberts 1968)	<i>Polyonyx gibbesi</i>			(Gore 1968)
zoeae I	coxopodite	1	1	zoeae I	coxopodite	naked	naked
	basipodite	1+2	1+2		basipodite	1+3(1+2)	1-2,3
	endopodite	2,2,2,10+1	2,2,2,10+1		endopodite	2,2,2,7-10+1	2,2,2,10+1
	exopodite	4	4		exopodite	4	4
zoeae II	coxopodite	1	1	zoeae II	coxopodite	naked	naked
	basipodite	1+2	1+2		basipodite	1+3(1+2)	1+3
	endopodite	2+I, 2+I, 2+I, 12+1	2+I, 2+I, 2+I, 14+I		endopodite	2+I, 2+I, 2+I, 8-12+I	2+I, 2+I, 2+I, 12+1
	exopodite	2+9	2+9		exopodite	11-12	12
<i>Petrolisthes armatus</i>			(Gore 1970)	<i>Porcellana sigsbeiana</i>			(Gore 1971c)
zoeae I	coxopodite	naked	naked	zoeae I	coxopodite	naked	naked
	basipodite	1+1	1+1 or 1+2		basipodite	1+2	1+2
	endopodite	2,2,1+2,5+1	2,2,1+2,5+1		endopodite	2,2,2,7+1	2,2,2,7+1
	exopodite	4	4		exopodite	4	4
zoeae II	coxopodite	naked	naked	zoeae II	coxopodite	1	1
	basipodite	1+1	1+1		basipodite	1+2	1+2
	endopodite	2,2+I, 1+2+I, 5+1	2,2+I, 1+2+I, 5+1		endopodite	2+I, 2+I, 2+I, 9+1	2+I, 2+I, 2+I, 9+1
	exopodite	3+12	12-15		exopodite	11-12	12

Meristic variations in telson setation, carapace armature and biramous appendages were noted as important taxonomic tools by Gurney (1938) and Lebour (1943), and continue to be useful in larval systematics. Even though variations in appendate setal counts alone may not be taxonomically significant, adequate analysis of such variations might be a method of distinguishing larvae from different populations of the same species (Gonor and Gonor 1973a). As more information is obtained, meristic variation may become even more significant in comparing decapod larvae of different genera or species.

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EFFECTS OF SALTWATER INTRUSION FROM THE INNER HARBOR NAVIGATION CANAL ON THE BENTHOS OF LAKE PONTCHARTRAIN, LOUISIANA

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ABSTRACT A study of the benthos of southern Lake Pontchartrain, Louisiana, was conducted from July 1976 to July 1978. Seven offshore stations and three stations in the New Orleans Marina complex were sampled seasonally. Offshore stations formed a transect from the Lake Pontchartrain Causeway to the Inner Harbor Navigation Canal (I.H.N.C.). A west to east gradient of increasing salinity and salinity stratification was evident.

Faunal differences among stations were assessed using indices of diversity, biological dominance, pollution, and station homogeneity. The fauna of the marina stations had a low species diversity and was dominated by annelids, indicative of a stressed environment. The fauna of stations near the I.H.N.C. were similar to the marina stations. Moving westward from the I.H.N.C., species diversity increased and the fauna became dominated by mollusks. Stressful conditions associated with the intrusion of water from the I.H.N.C. into Lake Pontchartrain appeared to be responsible for the faunal differences observed.

INTRODUCTION

The Lake Pontchartrain estuary has undergone numerous environmental changes associated with the activities of man. Among these changes are modifications in salinity regimes and increased levels of urban pollution.

The mean salinity of the southern sector of the estuary has increased since the construction of the Mississippi River

Gulf Outlet (Figure 1). Furthermore, this saltier water has been shown to have high concentrations of heavy metals, pesticides and other pollutants (Perret et al. 1971, Costa et al. 1977). The Bonnet Carré Spillway (Figure 1), which connects the Mississippi River to Lake Pontchartrain, was opened in 1973, 1975, and 1979. Each time, the salinity of the southern sector of the lake was temporarily reduced to less than 0.5 ppt (Poirrier and Mulino 1975, 1977). Various industrial pollutants were introduced into the lake from the Mississippi River (Perret et al. 1971).

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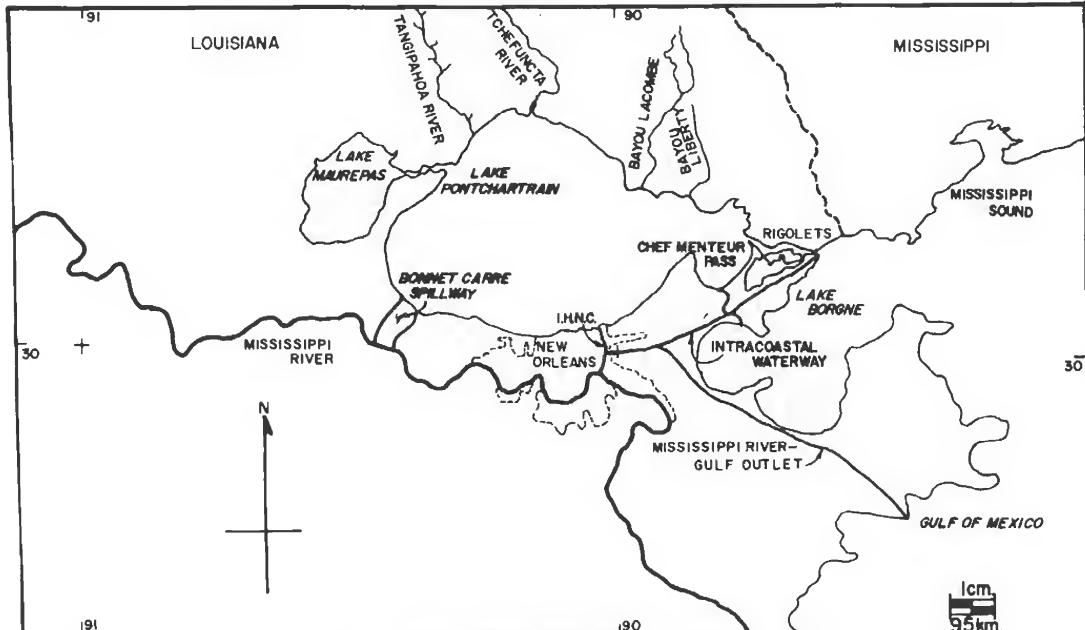


Figure 1. Map of Lake Pontchartrain, Louisiana, and vicinity.

Several studies (Stern and Atwell 1968, Stern and Stern 1969, Poirrier et al. 1975, Poirrier 1979a, Stone 1980) have established that storm water discharges into Lake Pontchartrain from the New Orleans Metropolitan Area result in high levels of total and fecal coliform bacteria, high concentrations of plant nutrients, and low dissolved oxygen (D.O.) values. Sikora and Sikora (1982) found a large area of bottom in southeastern Lake Pontchartrain to be desfaunaized.

The influence of the intrusion of water from the Inner Harbor Navigation Canal (I.H.N.C.) into Lake Pontchartrain was studied by Poirrier (1979b). He reported a west to east gradient of increasing salinity, salinity stratification, and decreasing bottom D.O. values. The present study was conducted to assess the impact of this non-mixing, higher salinity bottom water on the benthic community of southern Lake Pontchartrain. The marina complex was also sampled to provide information about the benthos of a highly stressed site. The effects of salinity stratification and resulting adverse water quality upon the benthos were evaluated by comparing sites along the salinity gradient to the marina sites.

MATERIALS AND METHODS

The areas sampled are shown in Figure 2. Stations were sampled seasonally from July 1976 to July 1978 using a

0.05 m² Eckman dredge. The samples were immediately preserved in 10% formalin. The goal of the sampling strategy was to obtain representative seasonal samples from each offshore station. However, a complete seasonal study was not possible because all stations were not accessible at all seasons due to rough weather. Samples taken at offshore stations A through G in July 1976, December 1976, and April 1977 were passed through a 1.0 mm sieve. Marina stations H through J were established in October 1977 and used for comparison with the offshore stations. In preliminary samples in the marina, however, few individuals were retained on the 1.0 mm sieve; therefore, a 0.125 mm sieve was used in subsequent sampling. Three replicate samples were taken from each station. No significant differences were found among the three samples using a completely randomized analysis of variance. Since there were no statistical differences among the three replicates, they were treated as one set of faunal data per station. During October 1977, April 1978, and July 1978, an extra sample was taken at each station (except station G), fixed in 10% formalin and analyzed for sediment size composition (Folk 1968).

Salinity, temperature and dissolved oxygen (D.O.) were measured 0.3 m from the surface and 0.3 m from the bottom at each station. Salinity and temperature were measured using a Beckman RS5-3 salinometer and D.O. was measured

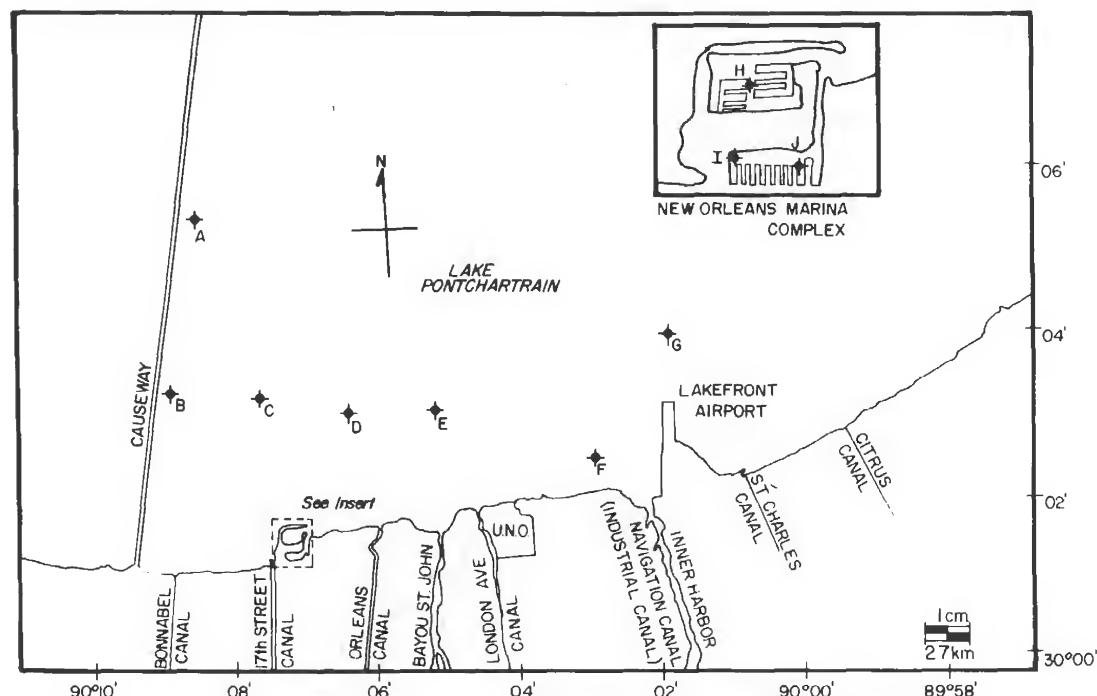


Figure 2. Map of study area in southern Lake Pontchartrain, Louisiana, showing sampling stations A–J.

with a YSI model 51A D.O. meter. Station depths were measured using a weighted chain marked in 1-m sections.

The faunal data was subjected to an analysis of species diversity, biological dominance, the degree of pollution based upon species abundance, and station homogeneity. Species diversity (H') was calculated using the Shannon-Weaver index (Shannon and Weaver 1962):

$$H' = - \sum (p_i \log_e p_i)$$

where p_i is the proportion of the i th species in each sample. An index of biological dominance (B.I.) was calculated by assigning the most numerous species in each sample five points, the next most numerous species four points, etc. These points were summed for all the samples and divided by the number of samples taken at each station (Fager 1957). Wass' pollution index (Wass 1967) assessed the degree of pollution at each station by measuring the ratio of stress-tolerant to stress-intolerant individuals at each station. Stress-tolerant species were considered to be those present in the marina complex, an area of poor water quality (Costa et al. 1977). Species abundances were also plotted against distance from the I.H.N.C. (Boesch 1971b). Sanders' index of faunal homogeneity (Sanders 1960), which is a measure of the percent of fauna common to a pair of stations, was calculated for all pairs of stations and arranged in a trellis diagram (McFayden 1963). Details of the sampling sites and methods employed are provided by Junot (1979).

RESULTS

Sediment composition at stations A through E was about 97% silt and clay. However, at station F the sediment was composed of 50% silt and clay, and 50% sand. Station F is near the I.H.N.C. in an area of swift currents. The marina stations H, I, and J had a high percentage (from 75 to 95%) of silt and clay, followed by sand.

Surface water salinity at offshore stations ranged from 2.5 ppt (Station C, April 1978) to 7.0 ppt (Station G, December 1976), with an overall mean of 4.2 ppt. Bottom water salinities at offshore stations varied from 2.5 ppt (Station B, April 1978) to 14.0 ppt (Stations E and F, October 1976), with an overall mean of 6.1 ppt. The average salinity in the marina complex was 3.5 ppt. The mean salinity profile (Figure 3) over the 2-year sampling period showed differences as large as 4.7 ppt between surface and bottom waters near the I.H.N.C. and negligible at the westernmost station. Thus, stratification of lighter, fresher water over the denser, saltier water introduced by the I.H.N.C. was most extreme at the eastern stations and decreased moving westward. Bottom water temperatures ranged from 10.7°C in December 1976 to 30.0°C in July 1976, with an overall mean of 22.3°C. Surface temperatures ranged from 11.2°C in December 1976 to 31.1°C in July 1976, with an overall mean of 23.1°C.

Surface D.O. values ranged from 4.3 ppm (Station J,

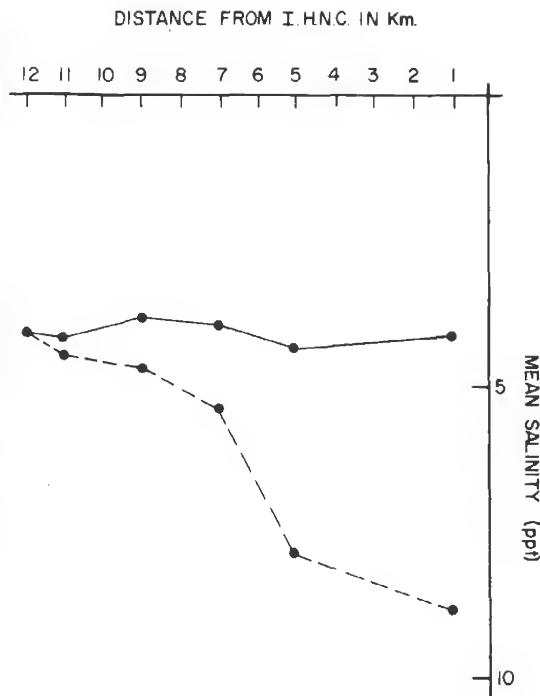


Figure 3. A graph of mean surface and bottom salinity values (ppt) versus distance from the I.H.N.C. (km) from stations A through F in southern Lake Pontchartrain, Louisiana, July 1976 to July 1978. Surface salinity is represented by a solid line whereas bottom salinity is represented by a dashed line.

July 1978) to 12.5 ppm (Station G, December 1976), with an overall mean of 9.3 ppm. Bottom D.O. values ranged from 0.5 ppm (Station C, July 1976) to 11.8 ppm (Station G, December 1976), with an overall mean of 6.9 ppm. The mean dissolved oxygen profile showed differences as large as 3.8 ppm between surface and bottom waters near the I.H.N.C. and as small as 0.8 ppm at unstratified stations (Table 1). Station depths ranged from 4.5 m (Stations A and B) to 10.5 m (Station F). Stations near the I.H.N.C. were deeper than stations near the Lake Pontchartrain Causeway (Figure 2).

A total of 29,643 individuals representing 33 taxa were collected (Table 2). Shannon-Weaver diversity indices were calculated for each sample (Table 3). Mean diversity was higher at unstratified stations A and B than at stratified stations E and F. In general, the pattern was one of decreasing diversity in an easterly direction. However, station C had a lower overall mean diversity than did station D; also, station G showed a low mean diversity. The overall mean diversity of stations A through F (1.115) was significantly higher ($\alpha = 0.05$) than the overall mean diversity of marina stations H through J (0.624).

TABLE 1.

D.O. (ppm) of surface and bottom waters at stations A-J in southern Lake Pontchartrain, Louisiana, July 1976 to July 1978.

Stations	July 76	Oct 76	Dec 76	Apr 77	Oct 77	Apr 78	July 78
A	* 8.0 5.4	-- --	-- --	-- --	9.6 9.2	8.5 7.5	7.9 8.6
B	8.8 6.4	9.4 6.2	11.5 11.3	9.3 8.9	9.6 9.6	9.0 1.0	8.5 8.5
C	8.2 0.5	9.2 6.5	11.3 11.2	9.7 8.8	-- --	8.5 8.4	8.3 7.5
D	8.8 4.4	10.2 3.2	11.5 11.5	9.8 7.7	-- --	8.4 7.8	7.9 7.5
E	9.6 2.2	11.0 4.1	11.8 11.5	10.2 6.6	9.4 5.5	-- 6.6	8.1 6.6
F	10.2 6.1	11.2 7.8	12.0 11.2	10.6 6.3	-- --	8.6 5.4	8.0 6.4
G	9.6 7.2	10.8 6.6	12.5 11.8	10.7 7.7	-- --	-- --	-- --
H	-- --	-- --	-- --	-- 8.0	8.2 6.3	8.1 5.8	8.7 5.8
I	-- --	-- --	-- --	-- 5.0	9.3 5.3	8.3 3.2	5.0 3.2
J	-- --	-- --	-- --	-- --	-- 6.0	8.2 2.2	4.3 2.2

*surface/bottom

TABLE 2.

Species list of benthic invertebrates from stations A-J in southern Lake Pontchartrain, Louisiana, July 1976 to July 1978.

Phylum Nematoda	Phylum Annelida	Phylum Arthropoda
	Class Polychaeta	Class Crustacea
	<i>Parandalia americana</i>	Subclass Cirripedia
	<i>Nereis occidentalis</i>	<i>Balanus improvisus</i>
	<i>Neanthes succinea</i>	Subclass Copepoda
	<i>Laeonereis culveri</i>	Order Calanoida
	<i>Pygospio elegans</i>	Subclass Malacostraca
	<i>Polydora websteri</i>	Order Isopoda
	<i>Streblospio benedicti</i>	<i>Edotea montosa</i>
	<i>Boccardia hamata</i>	Order Amphipoda
	<i>Ficopomatus miamiensis</i>	<i>Gitanopsis</i> sp.
	<i>Hobsonia florida</i>	<i>Melita</i> sp.
	Family Capitellidae	<i>Hyalella azteca</i>
		Order Mysidacea
	Class Oligochaeta	<i>Mysidopsis almyra</i>
Phylum Mollusca	Phylum Gastropoda	Order Decapoda
	<i>Texadina sphinctostoma</i>	<i>Rhithropanopeus harrissii</i>
	<i>Probythinella louisianae</i>	Class Insecta
	Class Pelecypoda	Order Diptera
	<i>Ischadium recurvum</i>	Family Chironomidae
	<i>Crassostrea virginica</i>	<i>Cryptochironomus</i> sp.
	<i>Congerius leucophæta</i>	<i>Coelotanypus</i> sp.
	<i>Mulinia pontchartrainensis</i>	<i>Dicrotendipes</i> sp.
	<i>Rangia cuneata</i>	Tribe Pentaneurini
	<i>Macoma mitchelli</i>	

TABLE 3.

Diversity, mean diversity for the first sampling period (X_1), mean diversity for the second sampling period (X_2), and overall mean diversity (\bar{X}) for stations A-J in southern Lake Pontchartrain, Louisiana, July 1976 to July 1978.

Stations	July 76	Oct 76	Dec 76	Apr 77	X_1	Oct 77	Apr 78	July 78	X_2	\bar{X}
A	1.210	--	--	--	1.210	1.073	1.603	1.192	1.289	1.269
B	0.926	1.381	1.003	1.006	1.097	1.471	1.507	1.159	1.379	1.217
C	0.421	1.101	1.108	0.880	0.887	--	1.387	1.591	1.489	1.081
D	1.241	0.620	0.872	1.044	0.944	--	1.476	1.479	1.475	1.122
E	0.239	0.562	1.006	1.073	0.719	0.937	1.515	1.133	1.195	1.078
F	0.630	--	0.827	1.162	0.873	--	0.909	1.074	0.992	0.920
G	0.486	0.646	0.583	0.696	0.603	--	--	--	--	--
H	--	--	--	--	--	1.012	1.069	0.980	1.020	--
I	--	--	--	--	--	0.716	0.815	0.108	0.546	--
J	--	--	--	--	--	--	0.560	0.049	0.305	--

The abundance of dominate species graphed as function of distance from the I.H.N.C. is shown in Figure 4. Dominate species were considered to be those which had a B.I. greater than or equal to 1. Changes in the species composition of the benthic community are apparent. The mollusks

Texadina sphinctostoma, *Rangia cuneata*, *Mulinia pontchartrainensis*, *Macoma mitchelli*, and *Probythinella louisianae* were more abundant at stations A and B, and decreased in importance with increasing salinity stratification near the I.H.N.C. The polychaetes *Streblospio benedicti*, *Hobsonia*

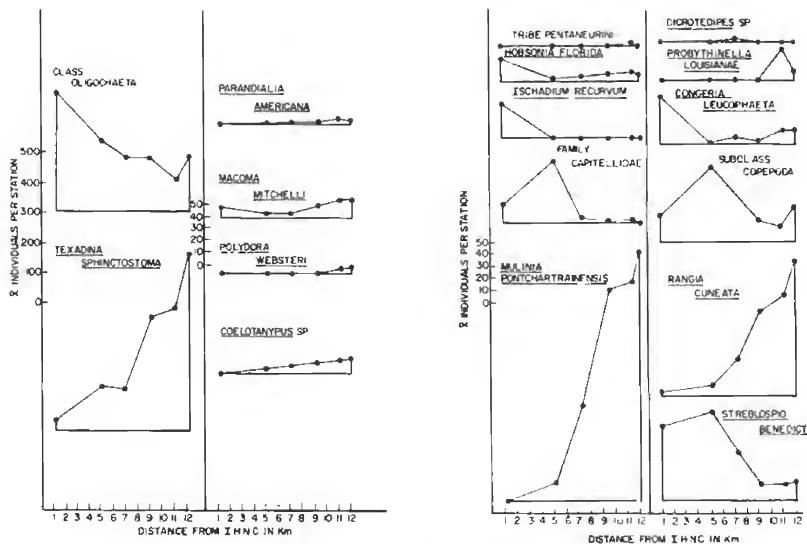


Figure 4. A graph of species abundance (as mean number of individuals per species per station) versus distance from the I.H.N.C. (in km) from stations A through F in southern Lake Pontchartrain, Louisiana, July 1976 to July 1978.

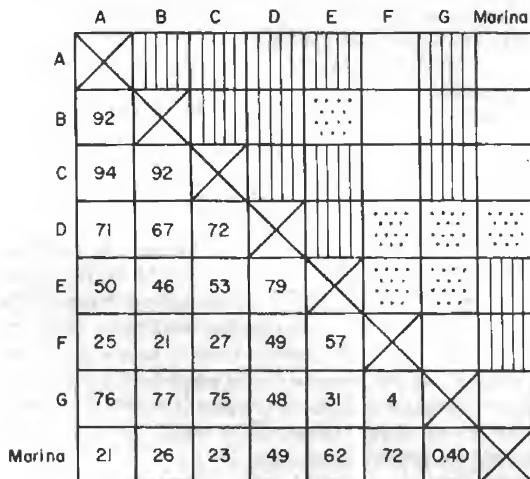


Figure 5. Trellis diagram of index of homogeneity. The percentage of species common to station pairs is presented numerically in the lower half, and schematically in the upper half of the diagram. Striped boxes indicate $>50\%$ homogeneity; the stippled boxes indicate 30–50% homogeneity, whereas the clear boxes indicate $<30\%$ homogeneity. The diagram includes data from stations A through G and the combined marina stations (H, I, and J) in southern Lake Pontchartrain, Louisiana, July 1976 to July 1978.

florida, capellids, and oligochaetes were more abundant at stratified stations E and F and decreased in abundance with decreasing stratification westward.

Sanders' index of faunal homogeneity (Sanders 1960) reflected the degree of faunal change along the salinity gradient

by measuring faunal similarity between pairs of stations in terms of species presence and abundance (Figure 5). Pairwise comparisons of unstratified stations A, B, and C showed high indices of similarity and a similar molluscan fauna. Only station F was highly distinct from the unstratified stations. Station F did, however, have affinities with stations D and E. Stations D, E, and F had a fauna either dominated by annelids or with a large annelid component. Stations D and E thus had affinities with the unstratified stations and with station F, whereas the fauna of station G was most like that found at the unstratified stations. The marina stations, which were characterized by poor water quality, showed the greatest degree of affinity with the stratified stations E and F. In terms of Wass' pollution index values (Table 4), stations A, B, and C constituted one group and stations D, E, and F constituted another. Stations D, E, and F showed a greater affinity to the polluted marina stations.

DISCUSSION

Salinity has been described as the major factor responsible for the distribution of estuarine organisms (Gunter 1961, Kinne 1966, Boesch 1977). Dissolved oxygen concentrations have also been found to affect the distribution and occurrence of benthic organisms, especially where stratification of the water column results in anoxic conditions in bottom waters (MacIntyre 1968, Coull 1969). Sanders (1960) found that sediment composition greatly influenced benthic distributions, but Muus (1967) felt that salinity and D.O. values were more important in determining the species composition of the benthos. In the present study, poor bottom water

TABLE 4.

Wass' pollution index for offshore stations A through F in southern Lake Pontchartrain, Louisiana, July 1976 to July 1978.

Station	Wass' Index
A	0.2854
B	0.2181
C	0.3201
D	1.0426
E	2.3707
F	4.7164

quality associated with salinity stratification appears to be a factor responsible for the distribution of benthic species.

Unstratified and marina stations had comparable salinity and substrate types, but their faunas were dissimilar. Unstratified stations had a fauna dominated by mollusks, whereas the marina stations had a fauna dominated by annelids. The stratified stations and the marina stations had different substrate types and different salinity values, yet they had a similar annelid fauna. Other studies have demonstrated that a shift from an estuarine fauna dominated by mollusks to one dominated by annelids occurs with increases in industrial and domestic pollution (Taylor et al. 1970, Crippen and Reish 1969, Pfitzenmeyer 1971, Richardson 1971, Boesch 1971a, 1971b). The change from a predominantly molluscan fauna at the westernmost stations to the predominantly annelid fauna at the easternmost stations indicates that stressful conditions were associated with salinity stratification.

Although a different mesh size (0.5 mm) was used in their sampling, the mean H' of offshore stations A-G ($H' = 1.042$) was similar to the mean H' of all stations ($H' = 1.086$) of Sikora and Sikora (1982). Station A ($H' = 1.269$) and station B ($H' = 1.217$) had higher H' values than the midlake station ($H' = 1.031$) of the Sikoras. Observed decreases in benthic diversity from west to east cannot be ascribed to a nearshore effect. Sikora and Sikora (1982) found higher diversity values at nearshore northwestern stations than at both their midlake station and their nearshore southern stations. Diversity values showed evidence of seasonal changes associated with salinity stratification and low D.O. concentrations. Summer and fall H' values were generally lower than spring and winter values (Table 3). Poirrier (1979b) demonstrated that salinity stratification in southern Lake Pontchartrain can extend into the fall, decreases with distance from the I.H.N.C., and is associated with low bottom D.O. concentrations. In the present study, low bottom D.O. concentrations were often reflected in low H' values. For example, stations C and E in July 1976 had low D.O. values and low H' values; during July 1978, D.O. concentrations and H' values were both higher. Dissolved oxygen concentrations on the bottom and in the sediments were probably

lower than those measured since measurements were made 0.3 m from the bottom. Several studies (Gauvin and Tarzwell 1952, 1956, Wilhm and Dorris 1966, 1968, Cairns and Dickson 1971) have used decreases in diversity indices to indicate decreasing water quality.

In studies conducted by Remane and Schlieper (1971), the oligohaline zone (0.5 to 5.0 ppt) in an estuary contained the lowest number of species. Moving into more saline waters, the number of species increased. Since stations E and F had bottom salinities ranging from 5.7 to 14.0 ppt, they might be expected to support a more diverse fauna than other offshore stations which had lower salinities. This was not the case; the diversity indices of stations E and F were generally lower than those of other offshore stations (Table 3). However, expectations of greater benthic diversity at higher salinity are based upon concepts developed by benthic ecologists working on homohaline or gradient estuaries in northwest Europe (see Boesch 1977). Most of the benthic species found in Lake Pontchartrain are estuarine endemics which are characteristic of gradient estuaries. Thus, fluctuating salinities (as in poikilohaline or fluctuating estuaries) in the area influenced by stratification could, in itself, have an adverse impact upon these endemic forms.

Gulf coast populations of the clam *Rangia cuneata* are only maintained within a salinity range of 0–15 ppt (Hopkins et al. 1973). *Rangia* and the snail *Probythinella louisianae* were absent from the far eastern area of Lake Pontchartrain in 1967 to 1973 (Tarver and Dugas 1973, Dugas et al. 1974) but present in 1978–1980 (Sikora and Sikora 1982). Their distribution may have been restricted by high salinity conditions prior to the 1973, 1975, and 1979 Bonnet Carré Spillway openings. The barnacle *Balanus subalbidus*, which dominates the epifauna of Lake Pontchartrain, was found to be limited to gradient salinity conditions below 16 ppt by Poirrier and Partridge (1979). Recent studies (Downs 1983) demonstrate that it has physiological adaptations which restrict it to low salinity waters. Little is known about the ecological and physiological factors which limit the distribution of estuarine endemics to low-salinity waters. As a group they do not appear to be able to readily adapt to rapid salinity changes in the high-salinity zone.

The differences in benthic fauna between stratified and unstratified stations and the similarity between the fauna of stratified and marina stations indicate that salinity stratification resulting from flow of more saline water from the I.H.N.C. has an adverse impact on the benthos of Lake Pontchartrain. This impact is probably caused by low bottom D.O. concentrations, changes from the normal salinity regime, and possibly toxic substances which accumulate in the non-mixing bottom waters.

Mean dissolved oxygen values presented in this study and Poirrier (1979b) were not low enough to account for the changes observed. However, D.O. concentrations in the sediments were probably lower and values were probably

lower at other times and exerted a limiting effect. The low H' values associated with low D.O. values in July and October 1976 indicate that low D.O. values do affect the benthos.

Saltwater intrusion may be having a direct impact on the benthos. Since the opening of the Mississippi River Gulf Outlet, the salinity regime has shifted from stable oligohaline conditions to rapidly changing salinities with occasional values above 15 ppt (Poirrier 1979b). This changed salinity regime may have depressed populations of Lake Pontchartrain endemics which are not adapted to this altered salinity regime. The expected colonization by euryhaline opportunists has not occurred but instead the high-salinity, stratified areas are dominated by tolerant forms found in stressed environments. Recruitment of euryhaline opportunists is probably limited because the source of saltwater is not adjacent estuaries but navigation canals with poor water quality and unnatural depth, bottom and salinity conditions.

Lake Pontchartrain receives a variety of pollutants from diverse sources (Costa et al. 1977). Toxic substances originating from the I.H.N.C., outfall canals, and the Mississippi River may accumulate in the non-mixing bottom layer and cause changes in community structure. Under anoxic conditions toxic compounds may be released from the sediments and H₂S produced.

Low D.O. concentrations, salinity stress, and toxic substances probably all affect the benthos. Additional information is needed on the concentration of toxic substances,

D.O. and salinity in bottom waters and sediments, and the biology of the benthos before definitive effects can be determined. However, the overall effect is caused by saltwater intrusion and salinity stratification. The impact on the benthos depends on the intensity, extent and duration of the stratification. This is dependent upon prevailing weather conditions. Stratification persists through summer and fall and is not disrupted by summer storms (Poirrier 1979b). The extent that D.O. is lowered depends on organic loading of the bottom layer. During years when plant nutrients and organic material are higher because of runoff and spillway openings, the D.O. concentration of the bottom layer will be lower. The extent of stratification depends upon the salinity of I.H.N.C. water and the movement of water from the I.H.N.C. into the lake. During periods of low flow, high salinity and temperatures, the I.H.N.C. probably becomes stratified and a bottom layer characterized by poor water quality develops. When this water enters the lake, an adverse impact on the benthos can be expected.

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COMMUNITY STRUCTURE OF DIATOMS EPIPHYTIC ON PNEUMATOPHORES OF THE BLACK MANGROVE, *AVICENNIA GERMINANS*, IN A LOUISIANA SALT MARSH

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ABSTRACT The taxonomy, diversity, and similarity of diatom assemblages epiphytic on pneumatophores of black mangrove, *Avicennia germinans* (L.) L., in southeastern Louisiana were investigated. A total of 109 taxa representing 27 genera were identified in samples from five sites. The most abundant taxa were *Nitzschia brittonii* Hagelstein, *Nitz. frustulum* (Kütz.) Grun., *Navicula diserta* Hust., *Denticula subtilis* Grun., and *Amphora tenuissima* Hust. Comparisons with previous studies indicate that the diatom flora epiphytic on *A. germinans* in this study is much more characteristic of temperate salt marshes than of subtropical mangrove communities.

INTRODUCTION

Studies of edaphic and epiphytic diatom assemblages of coastal Louisiana have been few. Maples and Watson (1979) reported several genera of edaphic diatoms associated with salt panes and surrounding angiosperm zones. Stowe (1980, 1982) investigated the vertical distribution of epiphytic diatoms on the culms of *Spartina alterniflora* Loisel. Cook and Whipple (1982) described the spatial and temporal distribution of edaphic diatom communities along a complex gradient from brackish to saline marshland. However, mangroves have not been previously sampled for epiphytic diatoms in Louisiana or from the Gulf coast of any other state.

The study of Navarro (1982) (Indian River, Florida) is the only report of diatoms epiphytic on mangroves in the continental United States. Outside the continental United States mangrove diatoms have been collected by Hagelstein (1938) in Puerto Rico, Reyes-Vásquez (1975) in Venezuela, Foged (1979) in New Zealand, and Sullivan (1981) from Bimini Harbor, Bahamas. The purpose of this investigation was to study the taxonomy, diversity and similarity of benthic diatom assemblages associated with the pneumatophores of the black mangrove, *Avicennia germinans* (L.) L., in Louisiana.

Description of study area

A. germinans has been observed in coastal Louisiana since the 1800's (Moldenke 1960). Present distribution is along canals and roadside ditches in the salt marshes of southeastern Louisiana.

Collections were made from five sites in two coastal salt marshes. Sites A, B, and C were near Fourchon City, Louisiana (Table 1). These sites were intertidal on a canal system connecting Bay Champagne to Bayou LaFourche. The ambient salinity was 25 ppt. Major angiosperm species associated with these sites were *Iva fructescens* L., *Distichlis spicata* (L.) Greene, and *Spartina alterniflora*. Sites D and E were along roadside ditches located on Grand Isle (Table 1) and

not subject to tidal fluctuations. Salinity at site D was 15 ppt; and at site E, 22 ppt. The major associated angiosperm species were *S. alterniflora*, *D. spicata*, *Salicornia bigelovii* Torr., and *Suaeda linearis* (Eli.) Moq.

TABLE 1.
Location of study sites in two salt marshes of
southeastern Louisiana.

Site	Longitude	Latitude
A	90° 11.3'	29° 06.9'
B	90° 10.5'	29° 07.2'
C	90° 10.2'	29° 07.4'
D	89° 59.4'	29° 13.8'
E	89° 59.6'	29° 14.2'

MATERIALS AND METHODS

Epiphytic diatoms were collected from *A. germinans* on February 20, 1982. A representative composite sample was collected at each site by scraping several exposed pneumatophores with a knife. Water column salinities were measured in the field with an A&O refractometer.

Each of the five composite samples was boiled first in HCl then boiled in HNO₃ with K₂Cr₂O₇ to oxidize all organic matter. A portion of each sample was mounted in Hyrax for identification and counting of diatoms with a Leitz Dialux 20EB light microscope. A sample consisted of exactly 500 valves from five counts of 100 valves where each count was made from a separate slide prepared from the composite sample. After each sample had been analyzed taxonomically, community diversity statistics were calculated. The Shannon-Weiner Information Index (Pielou 1975) was used as one measure of community diversity:

$$H' = - \sum_{i=1}^S \frac{n_i}{N} \log_2 \frac{n_i}{N},$$

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where H' (species diversity) is expressed as bits/individual, n_i is the number of valves of the i -th taxon, N is the total number of valves, and S is the total number of taxa in the sample. The second measure of community diversity calculated was redundancy (Main and McIntire 1974):

$$R' = \frac{H'_{\max} - H'}{H'_{\max} - H'_{\min}},$$

where

$$H'_{\max} = \log_2 S$$

and

$$H'_{\min} = \log_2 N - \frac{(N - S + 1)}{N} \log_2 (N + S + 1).$$

R' is a useful measure of the relative degree of dominance in the sample and has no units. Values of R' range from 0, when all taxa are equally common, to 1, when all taxa except one are represented by a single valve. Selected pairs of samples were compared using Stander's (1970) Similarity Index:

$$\text{SIMI} = \frac{\sum_{i=1}^S P_{ij} P_{in}}{\sqrt{\sum_{i=1}^S P_{ij}^2} \sqrt{\sum_{i=1}^S P_{in}^2}},$$

where P_{ij} and P_{in} are the proportion of the i -th taxon in the j -th and n -th samples respectively. SIMI has limits of 0 and 1. The larger the SIMI value, the greater the similarity between two samples. The niche breadth (B_i) of individual taxa was measured by the expression:

$$B_i = \exp \left[-\sum_{r=i}^Q \frac{n_{ir}}{N_r} \log_e \frac{n_{ir}}{N_r} \right],$$

where n_{ir} is the number of individuals of the i -th taxon found in the sample from the r -th site, and N_r the summation of individuals of the i -th taxon found at all Q sites (Levins 1968). B_i values can range from 1 to Q (= 5 in present study) and is a measure of how evenly distributed a given taxon is in the samples under consideration. B_i is not necessarily related to a taxon's total relative abundance in all samples.

RESULTS

A total of 109 taxa representing 27 genera were identified in the samples. The identity and relative abundance of each diatom taxon is listed in Table 2. The dominant four genera, in terms of numbers of taxa encountered, were *Navicula* (28), *Nitzschia* (26), *Amphora* (12), and *Achnanthes* (5). The dominant four genera, in terms of relative abundance, were *Nitzschia* (37%), *Navicula* (22%), *Amphora* (18%), and *Denticula* (10%). The five most abundant taxa epiphytic on *A. germinans*, in order of decreasing abundance, were as fol-

lows: *Nitzschia brittonii*, *Navicula diserta*, *Nitz. frustulum*, *Denticula subtilis*, and *Amphora tenuissima*. These five accounted for 58% of the 2500 valves counted. *Nitz. brittonii*, the most abundant diatom, was found only at sites A, B, and C and its limited distribution is reflected in its low B_i value of 2.73. Species of *Synedra* were abundant at sites D and E but not at sites A-C.

Each of the community diversity statistics listed in Table 3 was calculated from the data of Table 2. The highest species diversity value was found at site A (4.522) and the lowest, at site E (3.206). Redundancy was lowest at site D (0.300) and highest at site B (0.464). The largest number of species was found at site A (67) with the lowest at site E (36). No obvious differences in community diversity between sites A-C or sites D and E were apparent.

The highest degree of structural similarity (SIMI) existed between sites B and C (Table 4). These two sites shared 85.0% of the maximum similarity possible. The lowest SIMI value was between sites B and E. These sites shared only 15.5% of the maximum similarity possible. A somewhat surprising result was the relatively low SIMI value (0.478) for a comparison of the two Grand Isle sites. Sites A and B possessed the most taxa in common (34) and sites C and E the least (15) (Table 4).

Navicula tripunctata var. *schizonemoides* possessed the highest niche breadth (B_i) value but was represented by only nine valves in the samples (Table 2). With respect to the five most abundant taxa, only three were evenly distributed (i.e., $B_i > 4.00$). These were *Nitzschia frustulum* (4.58), *Denticula subtilis* (4.56), and *Navicula diserta* (4.20). B_i values for *Nitz. brittonii* and *Amphora tenuissima* were both < 3.00. A total of 56 taxa exhibited the minimum value of 1.00, since they were present in only one sample.

DISCUSSION

Of the 109 diatom taxa identified, 50 are new records for Louisiana. The dominant genera found on the pneumatophores of *A. germinans* in this study are the same ones reported by Stowe (1982) as epiphytes on *Spartina alterniflora* in a salt marsh north of my study area. With the exception of *Denticula*, the dominant genera from my study are the same found in edaphic salt marsh diatom assemblages in Mississippi by Sullivan (1978) and in Louisiana by Cook and Whipple (1982). A comparison of taxa in common with other studies revealed that 52% of the taxa reported by Stowe (1982), 59% of those reported by Cook and Whipple (1982) and 45% encountered by Sullivan (1978) were found in this study. It should be noted that Stowe (1982) reported only the dominant taxa. Fifty-three percent of the taxa found in the present study were also found in the *S. alterniflora* or *D. spicata* zones in a Mississippi salt marsh (Sullivan 1978). These two angiosperms were the most prominent ones associated with *A. germinans* in the study area. A comparison of the epiphytic diatom flora associated with *A.*

TABLE 2.

Relative abundance (expressed as number of valves in a sample of 500) and niche breadth values (B_i) of epiphytic diatom taxa on *A. germinans* in southeastern Louisiana. $\Sigma n_j = 5$ samples pooled as one.

Diatom taxon	Site						Diatom taxon	Site								
	A	B	C	D	E	Σn_j	B_i	A	B	C	D	E	Σn_j	B_i		
<i>Achnanthes brevipes</i>																
var. <i>intermedia</i> (Kütz.) Cl.	11	10	15	23		57	3.77									
<i>A. curvirostrum</i> Grun.					1	1	1.00	<i>N. capitata</i> var. <i>hungarica</i> (Grun.) Ross				1	1	1.00		
<i>A. hauckiana</i> Grun.	2		3	3		8	2.95	<i>N. circumtexta</i> Meister	1					1	1.00	
<i>A. lemmermanni</i> Hust.					7	7	1.00	<i>N. contenta</i> Grun.	35	2	1			38	1.55	
<i>A. temperei</i> M. Perag.	8	8	1			17	2.40	<i>N. creuzburgensis</i>								
<i>Amphirora paludosa</i> W. Sm.	1					1	1.00	Krasske	1					1	2.20	
<i>Amphora angusta</i> Greg.								<i>N. cryptocephala</i> Kütz	1	3	1			5	2.59	
var. <i>angusta</i>	4		8			12	1.89	<i>N. cryptolyra</i> Brockmann	1					1	1.00	
<i>A. angusta</i> var. <i>ventricosa</i> (Greg.) Cl.	1					1	1.00	<i>N. diserta</i> Hust.	23	88	44	125	36	316	4.20	
<i>A. caroliniana</i> Giffen	4			3	2	9	2.83	<i>N. hudsonis</i> Grun.	2	1		2	3	8	3.75	
<i>A. coffeiformis</i> Ag.	14	4	5	28	68	119	3.19	<i>N. incompodata</i> var. <i>minor</i> Hagelstein	3	1	29			33	1.39	
<i>A. exigua</i> Greg.	12		3	15	12	42	3.57	<i>N. marina</i> Ralfs						1	1.00	
<i>A. laevis</i> var. <i>perminuta</i>								<i>N. menisculus</i> Schum.	8	7	6	6	1	28	4.41	
Grun.	4					4	1.00	<i>N. obsoleta</i> Hust.	2	1				1	4.28	
<i>A. libyca</i> Ehr.		2				2	1.00	<i>N. pavillardii</i> Hust.		1	1			2	2.00	
<i>A. proteus</i> Greg.				1		1	1.00	<i>N. platyventris</i> Meister	1	1	3			5	2.59	
<i>A. sabyi</i> Salah	11		4			15	1.79	<i>N. salinarium</i> Grun.	2	1	1	3		7	3.59	
<i>A. tennerrima</i> Hust.	2	2		5		9	2.70	<i>N. salincola</i> Hust.	2	2		18	1	23	2.12	
<i>A. tenuissima</i> Hust.	29	2	4	26	174	235	2.30	<i>N. Schroeteri</i> Meister	1					1	1.00	
<i>Amphora</i> sp. No. 1				2		2	1.00	<i>N. subforcipata</i> Hust.						1	1.00	
<i>Bacillaria paixillifer</i>								<i>N. tenera</i> Hust.						1	1.59	
(Müll.) Hendey	6	4		7	3	20	3.80	<i>N. teneroides</i> Hust.						1	1.00	
<i>Berkelya rutilans</i> (Trent.) Grun.	2	1				3	1.89	<i>N. tripunctata</i> var. <i>schizonemoides</i> (V.H.) Patr.	2	2	2	2	1	9	4.86	
<i>Caloneis westii</i> (W. Sm.) Hendey			1			1	1.00	<i>N. yarrensis</i> Grun.						1	1.00	
<i>Cyclotella atomus</i> Hust.	1	2		2	1	6	3.78	<i>N. zostereti</i> Grun.	1	1	2			4	2.83	
<i>C. striata</i> (Kütz.) Grun.	1	2	2	3	1	9	4.59	<i>Navicula</i> sp. No. 1	1	1		2		4	2.83	
<i>Cylindrotheca gracilis</i> (Bréb.) Grun.	6					6	1.00	<i>Nitzschia apiculata</i> W. Sm.	1	2				4	2.83	
<i>Cymatosira belgica</i> Grun.		1				1	1.00	<i>N. bilobata</i> var. <i>ambigua</i>						18	3.16	
<i>Cymbella pusilla</i> Grun.	2					2	1.00	Manguin	2	4	10	2				
<i>Denticula subtilis</i> Grun.	71	26	55	23	66	241	4.56	<i>N. briortontii</i> Hagelstein	56	180	128			364	2.73	
<i>Diploneis weissflogi</i> (A.S.) Cl.					1	1	1.00	<i>N. closterium</i> (Ehr.) W. Sm.	1					1	1.00	
<i>D. interrupta</i> var. <i>caffra</i>								<i>N. communis</i> var. <i>hyalina</i>						2	4.20	
Giffen	1	8	30		1	40	2.06	Lund	3					1	4.75	
<i>D. pseudovalis</i> Hust.	1					1	1.00	<i>N. dissipata</i> (Kütz.) Grun.	4		2			2	2.83	
<i>Fragilaria construens</i>								<i>N. epithemoides</i> Grun.	2					2	4.00	
var. <i>venter</i> (Ehr.) Grun.	1	1		2	1	5	3.79	<i>N. fasciculata</i> (Grun.) Grun.	5	9	17	1		32	2.98	
<i>Gomphonema parvulum</i> Kütz.		1			1	4	2.83	<i>N. filiformis</i> (W. Sm.) Schütt	6	3	4			13	2.88	
<i>G. littoralis</i> Hendey				1		1	1.00	<i>N. frustulum</i> (Kütz.) Grun.	77	20	88	67	52	304	4.58	
<i>Gyrosigma beaufortianum</i> Hust.	1					1	1.00	<i>N. ganderscheimiensis</i>								
								Krasske	32	19	17	17	5	90	4.42	
<i>G. fascicola</i> (Ehr.) Cl.	1					1	1.00	<i>N. grana</i> Hohn & Hellerm.	1		1			2	2.00	
<i>G. hummii</i> Ilust.	1					1	1.00	<i>N. granulata</i> Grun.						1	1.00	
<i>G. peltoris</i> (Grun.) Hust.	1					1	1.00	<i>N. hungarica</i> Grun.	1	1		1	8	11	2.42	
<i>Mastogloia exigua</i> Lewis						1	1.00	<i>N. lorenziana</i> var. <i>subtilis</i>						1	1.00	
<i>M. pumila</i> (Grun.) Cl.	1			1	10	12	1.76	Grun.		1					1	1.00
<i>Melosira nummuloides</i> Ag.	4	4				8	2.00	<i>N. microcephala</i> Grun.						2	2.00	
<i>Navicula abunda</i> Hust.	6					6	1.00	<i>N. obtusa</i> W. Sm. var.								
<i>N. accomoda</i> Hust.	1					1	1.00	<i>obtusia</i>	1					1	1.00	
<i>N. aequorea</i> Hust.	1					1	1.00	<i>N. obtusa</i> var. <i>nana</i> Grun.	14	12	11			37	2.98	
<i>N. ammophila</i> Grun.	7	5	3	2	2	19	4.41	<i>N. palea</i> (Kütz.) W. Sm.		1				1	1.00	
								<i>N. panduriformis</i> var.								
								<i>continua</i> Grun.	1					1	1.00	
								<i>N. romana</i> Grun.				2	1	3	1.89	

TABLE 2 (Continued)

Relative abundance (expressed as number of valves in a sample of 500) and niche breadth values (B_i) of epiphytic diatom taxa on *A. germinans* in southeastern Louisiana.
 $\Sigma n_j = 5$ samples pooled as one.

Diatom taxon	Site					Σn_j	B_i
	A	B	C	D	E		
<i>N. romanaoides</i> Manguin	1	1	4			6	2.38
<i>N. sigma</i> (Kütz.) W. Sm.		1				1	1.00
<i>N. tryblionella</i> Hantz.				1		1	1.00
<i>N. vitrea</i> var. <i>salinarum</i>							
Grun.	4		8			12	1.89
<i>Nitzschia</i> sp. No. 1		1				1	1.00
<i>Opephora parva</i> (Grun.) Krasske		1				1	1.00
<i>Paralia sulcata</i> (Ehr.) Cl.			1			1	1.00
<i>Pleurosigma angulatum</i> (Quek.) W. Sm.	1					1	1.00
<i>P. salinarum</i> (Grun.) Grun.	1					1	1.00
<i>Psammodiscus niitidus</i> (Greg.) Round & Mann		4	3			7	1.98
<i>Rhopalodias gibberula</i> (Ehr.) Müll.				1		1	1.00
<i>R. musculus</i> cf. var. <i>producta</i> Grun.				9		9	1.00
<i>Stauroneis amphioxys</i> Greg. var. <i>amphioxys</i>	1					1	1.00
<i>S. amphioxys</i> var. <i>obtusa</i> Hendey	1					1	1.00
<i>S. legleri</i> Hust.	1					1	1.00
<i>Surirella atomus</i> Hust.			1			1	1.00
<i>Synedra affinis</i> Kütz.	2		10	1		13	1.99
<i>S. fasciculata</i> (Ag.) Kütz.			40			40	1.00
<i>S. demerarae</i> Grun.	2					2	1.00
<i>S. tabulata</i> var. <i>parva</i> (Kütz.) Hust.			23			23	1.00

TABLE 3.

Species diversity (H'), redundancy (R') and number of taxa (S) characterizing epiphytic diatom samples from *A. germinans* in southeastern Louisiana.

Statistic	Site				
	A	B	C	D	E
H'	4.522	3.617	3.902	4.027	3.206
R'	0.328	0.464	0.332	0.300	0.435
S	67	54	42	42	36

germinans from both Louisiana and Bimini Harbor (Sullivan 1981) showed only 18% of taxa in common, and the same value was found for a comparison with the epiphytic flora on red mangrove (*Rhizophora mangle* L.) prop roots in Indian River, Florida (Navarro 1982). The lack of similarity between this study and those of Sullivan (1981) and Navarro (1982) is not unexpected when one considers the lower lati-

TABLE 4.

Matrix of similarity values (upper right) and number of taxa in common (lower left) for comparisons for epiphytic diatom samples from *A. germinans* in southeastern Louisiana.

Sites	A	B	C	D	E
A		0.594	0.827	0.539	0.549
B	34		0.850	0.417	0.155
C	28	28		0.471	0.291
D	25	27	20		0.478
E	26	23	15	21	

tudes of their study areas.

Species diversity (H') and the number of taxa in a sample (S) are both high and similar to those reported by Sullivan (1978) and Cook and Whipple (1982) for Gulf coast salt marshes, but larger than those reported by Stowe (1982). H' and S for site A are among the highest reported in the literature and exceed those found for mangroves in Bimini Harbor by Sullivan (1981). Sites A, B, and C possessed the most similar epiphytic diatom assemblages (Table 4). With the exception of *Nitzschia brittonii*, the more abundant taxa were widely distributed across the five sites (Table 2). Discontinuous diatom distributions were due to the rare occurrences of many taxa (56 taxa were found at only one station), to unknown physicochemical differences among the habitats investigated and to stochastic processes. The first case supports the conclusion of Cook and Whipple (1982) that saline areas of southeastern Louisiana coastal marshes possess a large proportion of rare species. Comparisons with previous studies indicate that the diatom flora epiphytic on *A. germinans* in this study is much more characteristic of temperate salt marshes than of subtropical mangroves. The genus *Mastogloia* was poorly represented (only 2 species) in stark contrast to the subtropical studies of Sullivan (1981) and Navarro (1982). Most of the 109 taxa encountered are typical edaphic salt marsh diatoms. This finding lends some support to Sullivan's (1978) hypothesis that a uniform diatom flora may exist in salt marshes along the Atlantic and Gulf coasts of the United States. More importantly, this study represents the first report on epiphytic mangrove diatoms for the entire Gulf coast of the United States and Mexico, and is therefore valuable for distributional records and future, more comprehensive, work with this complex and diverse flora.

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Evaluation of a Leased Oyster Bottom in Mississippi Sound

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EVALUATION OF A LEASED OYSTER BOTTOM IN MISSISSIPPI SOUND

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ABSTRACT Twenty-four pairs of spat plates, strategically located on a 600-ha (1500-a) oyster lease, were monitored bi-weekly to determine the rate of oyster spatfall. Spatfall occurred from May 6 to July 31 and again from August 15 to October 24, 1979. The greatest spatfall occurred from August 15 to September 4, 1979. Data from shell bags that accompanied the spat plates indicated a maximum growth of 3.2 cm in two months. Oyster spat which attached to the planted cultch materials on the leases grew up to 7.9 cm during the 17-month sampling period, ending December 11, 1979. The lease area is capable of producing commercial-sized oysters in two seasons.

INTRODUCTION

During 1970, the Bureau of Marine Resources (formerly Mississippi Marine Conservation Commission) was granted statutory authority to lease water bottoms for the purpose of private oyster culture (49-15-27, Mississippi Code 1972, Chapter 15). Since then, techniques to improve the success of oyster culture on planted cultch have become a need of private lessees. Also, lending institutions need production and profit data before investing in mariculture endeavors. During 1979 and 1980, an Oyster Culture Demonstration Project, supported by the Mississippi Sea Grant Advisory Service, was conducted to document lease productivity. This manuscript is based on that project.

The purposes of the study were to determine: 1) the rate of oyster spatfall ($\text{no. m}^{-2} \text{ day}^{-1}$); 2) the subsequent oyster growth on planted cultch material; and 3) the location of spat-preference areas on a private oyster lease.

The spat sampling material used in this study was similar to that used in previous experiments (Cole and Knight-Jones 1939, Butler 1955, Shaw 1967). Smooth, artificial materials, such as asbestos plates, cement board, and slate, have been used for quantification of spatfall, since determining spatset on irregularly shaped and textured shells is difficult. Such material is usually cut into squares of a particular size and deployed in pairs in the water. The plates can be made to approximately equal areas of the inner faces of oyster shells. Previous data revealed a close similarity of trends in setting on the two substrates (Shaw 1967). The under-surface of the plates especially attract the negatively phototoxic oyster larvae (Galtstoff 1964, Ritchie and Menzel 1969).

Fouling on newly planted cultch material is detrimental to spatset. Hoese et al. (1972) discovered that the barnacle (*Balanus eburneus* Gould) set on asbestos plates was 78 times that of oysters in Mobile Bay, Alabama. Encrusting bryozoans (i.e., *Membranipora* spp. and *Electra* spp.) can also cause serious fouling, thus delaying cultch planting until

oyster setting is imminent (Beaven 1947). Another bryozoan (*Bowerbankia gracilis* Leidy) was found to secrete metabolites which were detrimental to oysters (MacKenzie 1970). McGraw (1980) also found that barnacles and colonial bryozoans compete with oyster larvae for setting space in Mississippi Sound.

Leases at Bellefontaine Point (Figure 1) may be excellent for oyster culture because of their proximity to Biloxi and Pascagoula bays, where large oyster reefs exist. Eleuterius (1976) reported that the core of the discharge from the West Pascagoula River follows the shoreline westward past Grave-line Bayou, then southward (over the lease area), exiting the Sound through Dog Keys Pass. He also found that during certain times of the year, Biloxi Bay's outflow merges with water from the West Pascagoula River south of Bellefontaine Point. Because of the higher salinity of the central and eastern Mississippi Sound, few areas that appear suitable for oyster culture occur outside of existing natural oyster reefs; however, one area that should receive serious consideration is south of Bellefontaine Point (Eleuterius 1977).

MATERIALS AND METHODS

Spat sampling apparatuses consisted of two $10 \times 10 \times 0.6$ -cm asbestos plates held apart by a 0.6-cm piece of PVC pipe (1.25 cm diameter), suspended through the center with polypropylene rope (0.6-cm diameter) (Figure 2). A wire pin was used in one corner to prevent plate-to-plate rotation. One set of spat plates was positioned at each of 24 wooden pilings which marked the corners of 15 40-ha (100-a) leases (approximately 400 m south of Bellefontaine Point (Figure 2)). The plates were anchored to pilings at the waterline and to a shell bag, resting on the bottom. Fortnightly monitoring of the plates occurred from April 16 through October 24, 1979. The plates were collected, rinsed with tap water and air dried. The plates (both sides) were examined with a 7X dissecting stereomicroscope. Oyster spat were counted and recorded as the number of spat set per m^2 per day, using the formula:

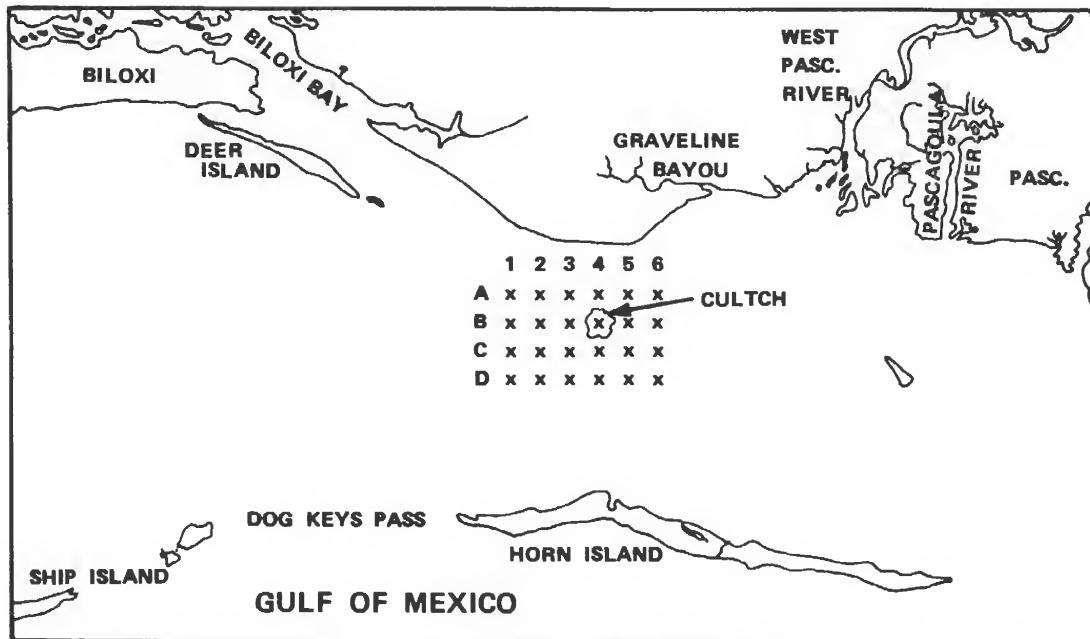


Figure 1. Map of lease area (x denotes corner piling).

$$\frac{\text{Total no. spat} \div \text{Total no. plate sides } (100 \text{ cm}^2/\text{side})}{\text{Total no. days exposed}} \times 100$$

Plates were scraped with a putty knife, cleaned with a wire brush and reused for subsequent collection periods.

The shell bags consisted of 1.9-cm (mesh size) Dupont Vexar® cylindrical webbing containing 0.015 m³ (0.5 ft³) of washed oyster shells. Fresh bags were placed on the leases from June 1 to July 31, 1979 and from July 31 to December 11, 1979, which coincided with spring and fall spawning periods, respectively. After collection, each bag was tagged, rinsed with tap water and air dried. Spat on individual oyster valves were counted with a 2X desk lens.

Bottom and surface water temperatures and salinities were determined during every sample collection. A hand-held mercury thermometer and a refractometer (Model AM 126, AO Instrument Company) were used.

The leaseholder (E. R. Gollott, Cap'n Gollott Seafood, Biloxi, Mississippi) planted approximately 2080 m³ of cultch material (*Rangia* clam shells) on June 1, 1979. A 0.4-ha (1-a) plot was established over the planted shells using four corner poles placed 35.9 m (118 ft.) from a center pole in north, south, east, and west directions.

Oysters from the 0.4-ha plot were sampled on May 7 and November 11, 1980. Three 0.5-m² samples were collected along each of the north, south, east, and west transects from the center. The samples were analyzed for oyster data including: 1) total number alive; 2) size range; 3) mean size;

4) total number dead; and 5) percent mortality. Live oysters were measured and grouped in 1.0-cm categories ranging from 0.0–0.9 to 7.0–7.9 cm. All detached left valves and empty boxes were counted as dead oysters. Predators were also noted by species and prevalence.

RESULTS

Spatfall Analyses

Data indicated that spatfall occurred from approximately May 6 through July 31, and again from August 15 through October 24, 1979 (Table 1). I believe, however, that spatfall occurred beyond October, since small, live spat (0.8 cm) were found on cultch material collected on December 11, 1979. Smaller spat (0.2 cm) were also found on shell bag cultch collected the same day. The heaviest spatfall over the entire lease area occurred from August 15 to September 5, followed by a similar peak the following two weeks (Tables 1, 2, and 3). Peak spatfall for the spring spawning occurred from June 16 to July 31, 1979 (Tables 1 and 4). A two-way analyses of variance (Steel and Torrie 1980) revealed no statistically consistent north-south or east-west preference for spatfall over the lease area (Tables 2, 3, and 4). Data collected from August 15 to September 5, however, produced an F-value significantly higher than the 99th percentile, showing a possible north-south preference of spatfall for that time period (Table 2).

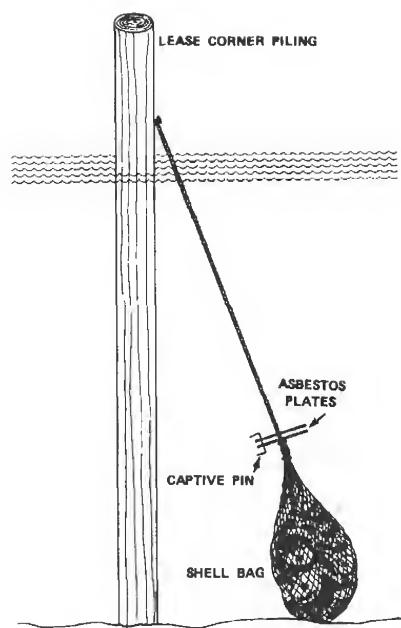


Figure 2. Spat plate-shellbag sampling apparatus.

Cultch Analyses

Cultch samples produced data verifying that good oyster growth is possible in a short period of time in Mississippi Sound. Data from shell bags showed growth of up to 3.2 cm in two months (June 1–July 31) and 4.2 cm in five

TABLE 1.
Spat plate data from April 4 to October 24, 1979.

Dates	Total no. spat	Total no. plates used	Total no. spat per m ² per day	(ppt)	Bottom salinity range	Average bottom temperature (°C)
04 Apr-17 Apr	0	48	0.0	2-12	21.0	
17 Apr-06 May	0	48	0.0	6-18	22.0	
06 May-20 May	2	48	0.14	4-12	25.0	
20 May-01 Jun	23	48	1.99	8-15	26.5	
01 Jun-16 Jun	17	48	1.18	12-20	27.5	
16 Jun-03 Jul	190	46	11.47	14-21	30.0	
03 Jul-17 Jul	10	48	0.74	18-22	30.0	
17 Jul-31 Jul	14	48	1.04	7-17	30.0	
31 Jul-15 Aug	0	48	0.0	16-19	30.0	
15 Aug-05 Sep	5196	46	268.94	19-22	—	
05 Sep-24 Sep	4600	46	263.15	11-15	22.0	
24 Sep-24 Oct	265	14	31.54	20-23	20.0	

months (July 31–December 11, 1979).

The first cultch sampling (May 7, 1980) from the 0.4-ha plot also indicated good oyster growth. The maximum oyster size was 5.2 cm (Table 5). The mean size was relatively the same from all four sampled areas, ranging from 1.82 to 2.29 cm. Samples from the eastern area produced the highest density (318/0.5 m²) and the lowest mortality, with 56% of the live oysters falling in the 1.0- to 1.9-cm size category (Table 5). The mean oyster size from all of the 0.5-m² samples was 2.0 cm, with a mean density of approximately 139 oysters/0.5 m². The 1.0- to 1.9-cm size category produced the highest percentage of the total (51.6%). The mortality averaged 19.5%; however, most of the dead oysters were in the 0.0- to 0.9-cm size range.

The data from the second cultch sampling (November 11, 1980) from the 0.4-ha plot indicated another spatfall during that year along with an increase in the size range. The mean size from the four areas on the plot ranged from 2.3 to 2.9 cm (Table 6). The largest oyster was 7.7 cm. The spatfall that occurred during 1980 accounted for >17.9% of all oysters measured. The eastern area produced the highest density (318/0.5 m²) and the lowest mortality (11.9%), with the 1.0- to 1.9-cm category contributing 56% of the total. For all areas, the mean oyster size was 2.0 cm, with a mean density of approximately 141.3/0.5 m². The 2.0- to 2.9-cm category produced the highest percentage of the total 51.6%.

DISCUSSION

Spatfall Analyses

This study indicated no preference in spatfall settling within the lease area. Table 1 clearly shows, however, the occurrence of two spatfall periods (May 6 to July 31 and August 15 to October 24). The double-spawning of oysters along the Gulf has been known since it was discovered by Hopkins (1931) in Galveston Bay, Texas. He found spatfall to be dependent on temperature and salinity. Based on previous studies which found that 3 to 25 spat/shell constitute a commercial spatset (Lindsay et al. 1958, Quayle 1958), a spatfall of commercial intensity occurred during the study period.

Cultch Analyses

Obtaining a representative sample from an oyster reef using quadrat samples is difficult. Ogle (1980) reported that 40 replicate quadrat samples from the Biloxi Bay reef produced a fluctuating cumulative mean. The mean-to-variance ratio for the quadrat samples was greater than one (18.72) indicating a patchy oyster distribution and inadequate sample size. During this study, the mean number of oysters/0.5 m² quadrat sample was 176.2 oysters (Table 6), but the standard deviation was equal to half of the mean (± 85.12). The high deviation indicates that more sampling is necessary; however, the value of the 0.4-ha reef can still be estimated. By extrapolation, the number of oysters on

TABLE 2.
Spatfall data from individual corner pilings during August 15 to September 5, 1979 (x denotes lost sample).

	1	2	3	4	5	6	Total	No. per m ² per day
A	40	54	52	135	63	156	500	99.2
B	87	152	121	65	349	128	902	178.9
C	146	149	613	x	363	757	2028	482.8
D	141	51	345	486	518	225	1766	350.3
Total	414	406	1131	686	1293	1266		
No. per m ² per day	123.2	120.8	336.6	272.2	384.8	376.7		
ANOVA = Analysis of Variance								
North-South F = +6.733 (3.29 α = 0.05; 5.42 α = 0.01); East-West F = +2.112 (2.9 α = 0.05; 4.56 α = 0.01)								

TABLE 3.
Spatfall data from individual corner pilings during September 5 to September 24, 1979 (x denotes lost sample).

	1	2	3	4	5	6	Total	No. per m ² per day
A	24	327	815	534	383	214	2297	503.7
B	54	36	108	7	191	472	868	190.3
C	93	22	82	x	90	221	508	133.6
D	271	62	61	85	47	401	927	203.3
Total	442	447	1066	626	711	1308		
No. per m ² per day	145.3	147.0	350.0	274.5	233.8	430.2		
North-South F = +2.963 (3.29 α = 0.05; 5.42 α = 0.01); East-West F = +0.897 (2.9 α = 0.05; 4.56 α = 0.01)								

TABLE 4.
Spatfall data from individual corner pilings during June 16 to July 3, 1979 (x denotes lost sample).

	1	2	3	4	5	6	Total	No. per m ² per day
A	5	6	19	3	8	15	56	13.7
B	12	20	14	x	6	6	58	17.0
C	6	5	11	1	19	9	51	12.5
D	6	7	4	2	2	4	25	6.1
Total	29	38	48	6	35	34		
No. per m ² per day	10.6	13.9	17.6	2.9	12.8	12.5		
North-South F = +2.077 (3.29 α = 0.05; 5.42 α = 0.01); East-West F = +0.869 (2.9 α = 0.05; 4.5 α = 0.01)								

the plot is $1,409,600 \pm 680,960$. At 400 oysters/\$10 bushel and commercial-sized oysters in two seasons, the 0.4-ha reef would be worth approximately $\$35,240 \pm \$17,024$, barring high mortality. In fact, high mortality did occur on the reef during the summer of 1981, primarily because of predation by the southern oyster drill (*Thais haemastoma*).

Current lease production

Low production is characteristic of private leases in Mississippi waters. Currently, 772.8 ha (1908.24 a) are leased; however, less than 1% of the commercial oyster harvest is from private oyster leases (*fide*, Thomas VanDevender, Bureau of Marine Resources, Long Beach, Mississippi). The

majority of production from these areas has been from the relaying of polluted oysters.

Lease productivity could be increased in a number of ways, all of which require intensive harvesting techniques. Once cultch material is planted, this initial investment is usually left unattended. The cultch, in the mean time, attracts crabs, fish, and commercial and recreational fishermen. By harvesting the commercial species attracted to the reef, an income from the initial investment could be immediately realized.

High oyster mortality is caused primarily by oyster drill predation. Recent shell plantings at the Round Island and Whitehouse areas by the Bureau of Marine Resources were

TABLE 5.

Pooled data from three 0.5-m² cultch samples collected from four, separate lease-plot areas, May 7, 1980.

Area	Total no. alive	Total no. alive within size categories (cm)					Size range (cm)	Mean size (cm)	Total no. dead	% Mortality	
		0.0-0.9	1.0-1.9	2.0-2.9	3.0-3.9	4.0-4.9					
North	368	45	161	102	33	25	2	0.5-5.1	1.98	92	19.9
South	70	4	26	17	9	11	3	0.6-5.2	2.29	31	30.6
East	954	53	535	320	34	11	1	0.5-5.0	1.82	130	11.9
West	277	14	140	101	21	1	0	0.6-4.3	1.91	74	21.0
% of total		6.9%	51.6%	32.3%	5.8%	2.9%	0.5%				

TABLE 6.

Pooled data from three 0.5-m² cultch samples collected from four separate lease-plot areas November 11, 1980.

Area	Total no. alive	Total number alive within size categories							Size range	\bar{X} size	No. dead	% Mortality	
		0.0-0.9	1.0-1.9	2.0-2.9	3.0-3.9	4.0-4.9	5.0-5.9	6.0-6.9					
North	323	53	63	95	44	37	20	10	1	0.3-7.3	2.6	47	12.7
South	356	74	88	108	27	40	11	7	1	0.3-7.1	2.3	67	15.8
East	273	35	45	69	52	36	25	8	3	0.5-7.7	2.9	52	16.0
West	316	65	61	88	46	29	23	4	0	0.1-6.1	2.4	56	14.6
% of total		17.9%	20.3%	28.4%	13.3%	11.2%	6.2%	2.3%	0.4%				

decimated by drill infestation (*fide*, William Demoran, Gulf Coast Research Laboratory, Ocean Springs, Mississippi). Locating a lease near a freshwater source is generally used to combat this high-salinity predation; however, poor water quality caused by land runoff usually occurs. The only other alternative is to raise the oysters off the bottom, away from the drill predation, using lantern nets, Nestier® trays, Vexar® bags, or "chicken coops" (Supan 1981). The cost of this type of intensive culture could be defrayed by utilizing commercial species as previously mentioned.

In conclusion, present lease productivity in Mississippi Sound would not promote interest for financial backing by lending institutions, as hoped for by the Oyster Culture Demonstration Project. High spatfall and subsequent good oyster growth indicates a potential for high yields. A greater effort in farming a lease could produce a profit, provided

the lessee utilized all of the available resources. In any event, oyster farming is considered a high risk investment.

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Tanaidacea (Crustacea: Peracardia) of the Gulf of Mexico. III. On the Occurrence of *Teleotanais gerlachi* Lang, 1956 (Nototanaidae) in the Eastern Gulf

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TANAIDACEA (CRUSTACEA: PERACARIDA) OF THE GULF OF MEXICO. III. ON THE OCCURRENCE OF *TELEOTANAIIS GERLACHI* LANG, 1956 (NOTOTANAIDAE) IN THE EASTERN GULF

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ABSTRACT *Teleotanais gerlachi* Lang, 1956, a euryhaline member of the family Nototanaidae, known from Brazil and El Salvador, is reported from the eastern Gulf of Mexico (west coast of Florida) and the west coast of Africa (Nigeria). The species is diagnosed and illustrated. Differences between *Teleotanais* and the superficially similar genus *Paratanais* (Paratanaidae) are briefly compared and discussed.

Knowledge of the distribution and systematics of members of the family Nototanaidae is very fragmentary. Of the genera so far established, *Nototanais* Richardson, 1906, seems to be restricted to the Antarctic-Subantarctic region and another, *Tanaissus* Norman and Scott, 1906, inhabits the shallow waters of the North Atlantic as well as the North Pacific. The remaining genera are monotypic. *Androtanais* Sieg, 1973; *Metatanais* Shiino, 1952; and *Protatanissus* Sieg, 1983, are known only from their respective type-localities. *Teleotanais* Lang, 1956, has been reported previously only from the coasts of El Salvador and Brazil. During our recent studies on the tanaidacean fauna of the Gulf of Mexico we discovered specimens of *Teleotanais gerlachi* Lang, 1956, from a sample collected by D. Bishop from the west coast of Florida. We also had access to specimens of *T. gerlachi* collected from the west coast of Africa (Nigeria) and this record is also included here.

Teleotanais gerlachi Lang, 1956
(Figures 1–3)

Synonymies: see Sieg, 1983: 418–419.

Material Examined – 11 ♀♀ (10 ♀♀ in coll. Heard, 1 ♀ in coll. Sieg, dissected) from Crystal River, Florida (28°55'N, 82°40'W); Highway 40 off US Highway 19, 4 miles west of Yankeetown, from oyster rock [together with 4 specimens of *Hargeria rapax* (Hargen 1918); D. Bishop, collector. Approximately 200 specimens (neuters, females) from Elechi Creek near Port Hartcourt, Nigeria (04°47.3'N, 06°58.6'E); high intertidal, on *Avicennia* pneumatophores, among green algae and *Bostrychia*, mesohaline; co-occurring with *Sinellulus standfordi* (Richardson, 1901); C. B. Powell, collector].

Diagnosis – Antenna I 4-jointed, first joint at most

twice as long as second, fourth joint relatively short with 2 aesthetascs at tip (Figure 1); antenna II 6-jointed, third joint elongate (Figure 1); maxilla 1 with 11 spines (Figure 2); basis of maxilliped totally fused (Figure 1); propodus of pereopods with 1–3 distal setae, 2 long sternal setae and 1 short tergal seta; basis of pereopods 4–6 thickened (Figure 3); endopodite of pleopods narrowing at junction with basis, without a lateral marginal seta, separated from others by a gap (Figure 1); uropods biramous, endopodite and exopodite 2-jointed, exopodite longer than first joint of endopodite (Figure 1).

Remarks – *Teleotanais* superficially resembles *Paratanais* Dana, 1852, because both genera have a 4-segmented antenna I and uropods with 2-jointed exopodite and endopodite. In *Paratanais* the last joint of antenna I is elongate and longer than the second and third joint combined, while in *Teleotanais* the last joint is distinctly shorter. Another difference is found in antenna II which in *Paratanais* has a short, thick third joint with strong outer spine, while in *Teleotanais* the third joint is elongate (as long or longer than the fourth joint) and lacks an outer spine. Maxilla 1 bears in *Teleotanais* eleven and in *Paratanais* nine terminal spines. The maxillipeds of the two genera are distinctly different. Since *Paratanais* belongs to the Family Paratanaidae the basis of the maxilliped is unfused; whereas it is completely fused in *Teleotanais* (Nototanaidae). Additionally in *Paratanais* the endite of the maxilliped is broad and expanded laterally, fused with the basis (Sieg 1981: 1274 Figure 2). In *Teleotanais* the endite is small and of normal shape with a relatively long seta at the outer margin of the endite, which we believe to be a characteristic of this genus. The pleopods of *Teleotanais* and *Paratanais* are distinctly different. In *Teleotanais* specialized setae on the distal part of the exopodite and the separate seta inserted proximally at the outer margin of the exopodite are missing; these setae are present in *Paratanais* and all other genera in the Paratanaidae. The chela of the chelipeds of *Teleotanais* and *Paratanais* also have distinctly different shapes.

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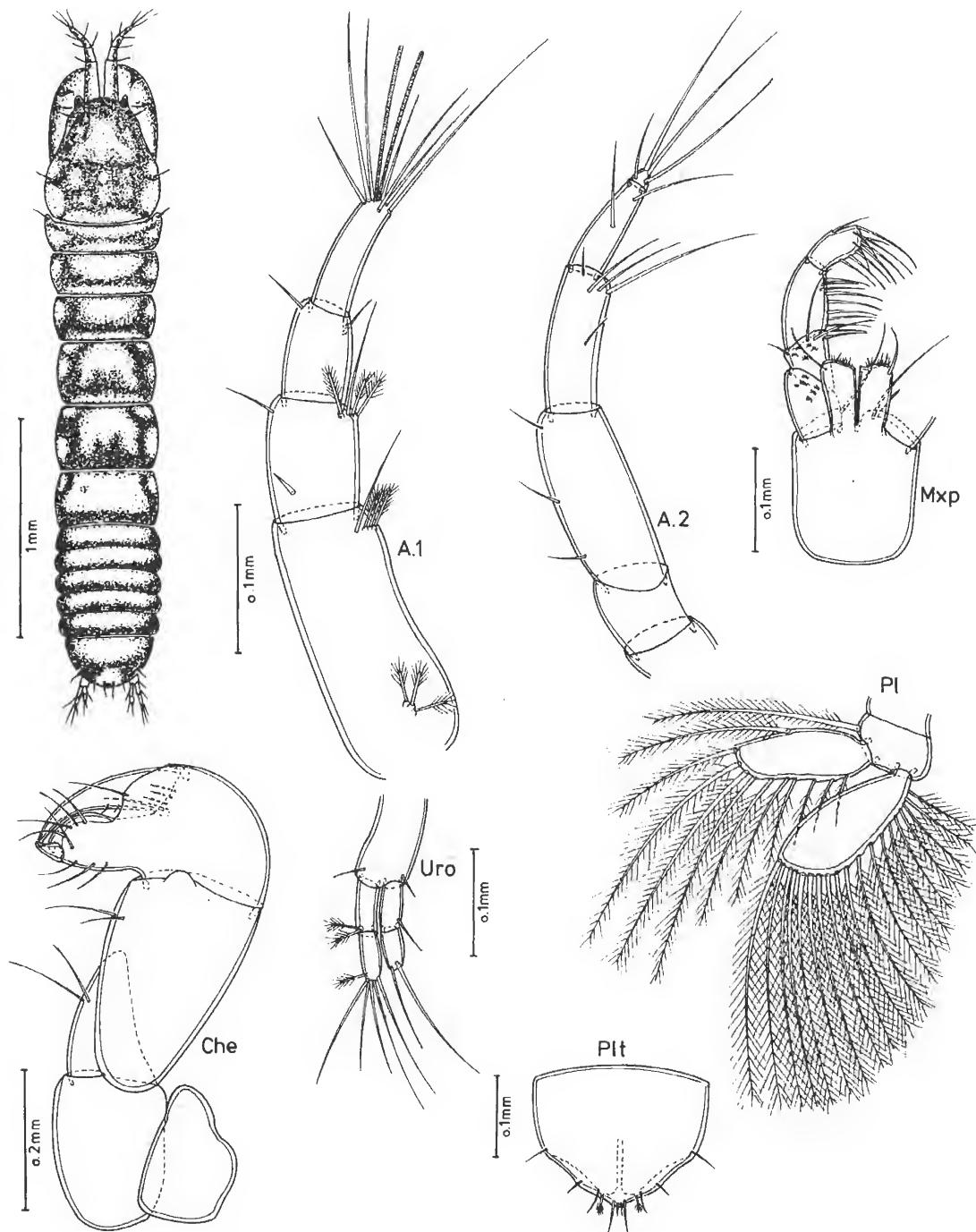


Figure 1. *Teleotanais gerlachi* (dorsal view of female). A. 1 = antenna I; A. 2 = antenna II; Mxp = maxilliped; Che = chela; Uro = uropod; Pl = pleopod; Plt = pleotelson.

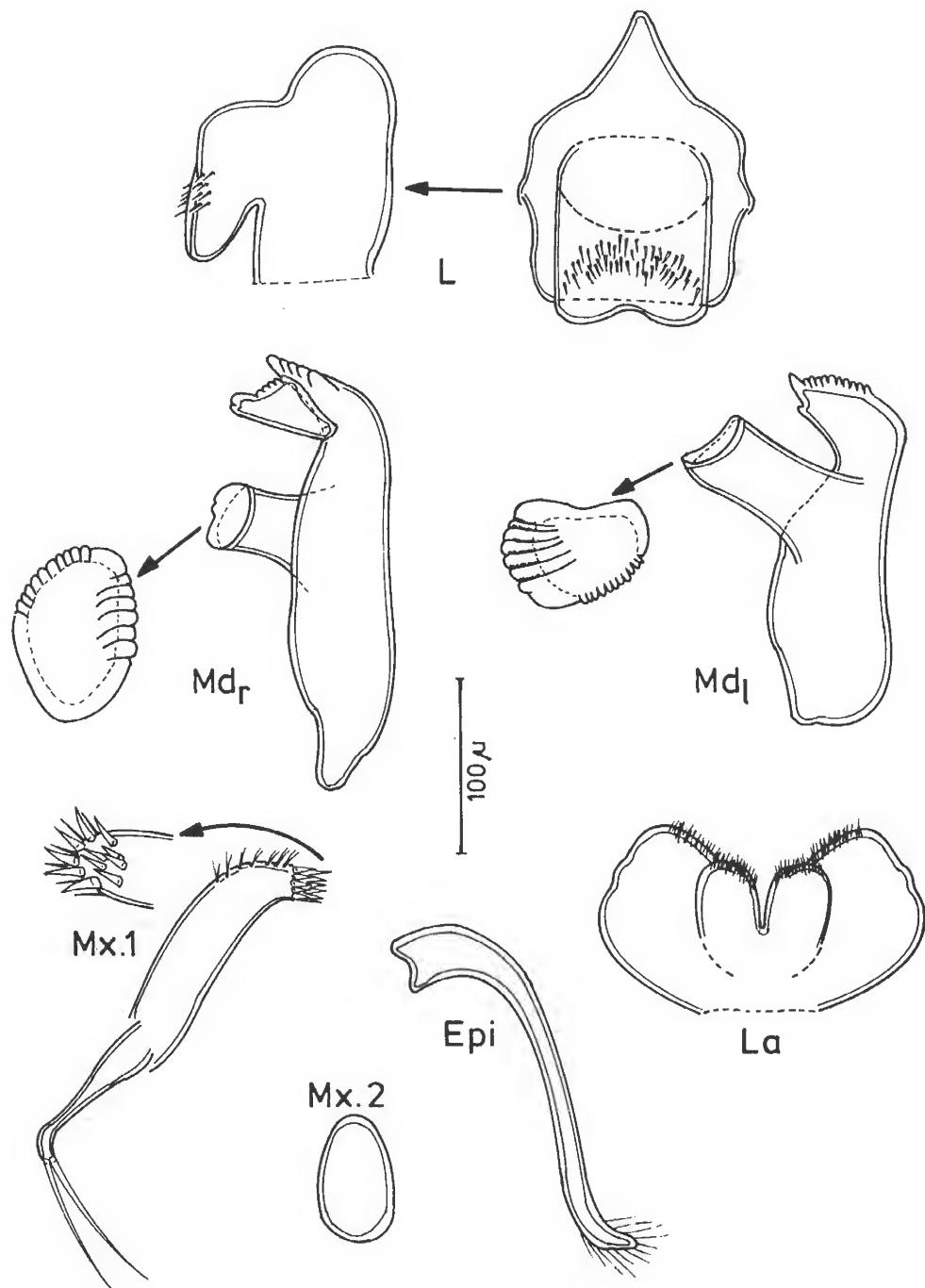


Figure 2. *Teleotanais gerlachi* (female). L = labrum; Md_r = right mandible; Md_l = left mandible; Mx. 1 = maxilla 1; Mx. 2 = maxilla 2; Epi = epipharynx; La = labium.

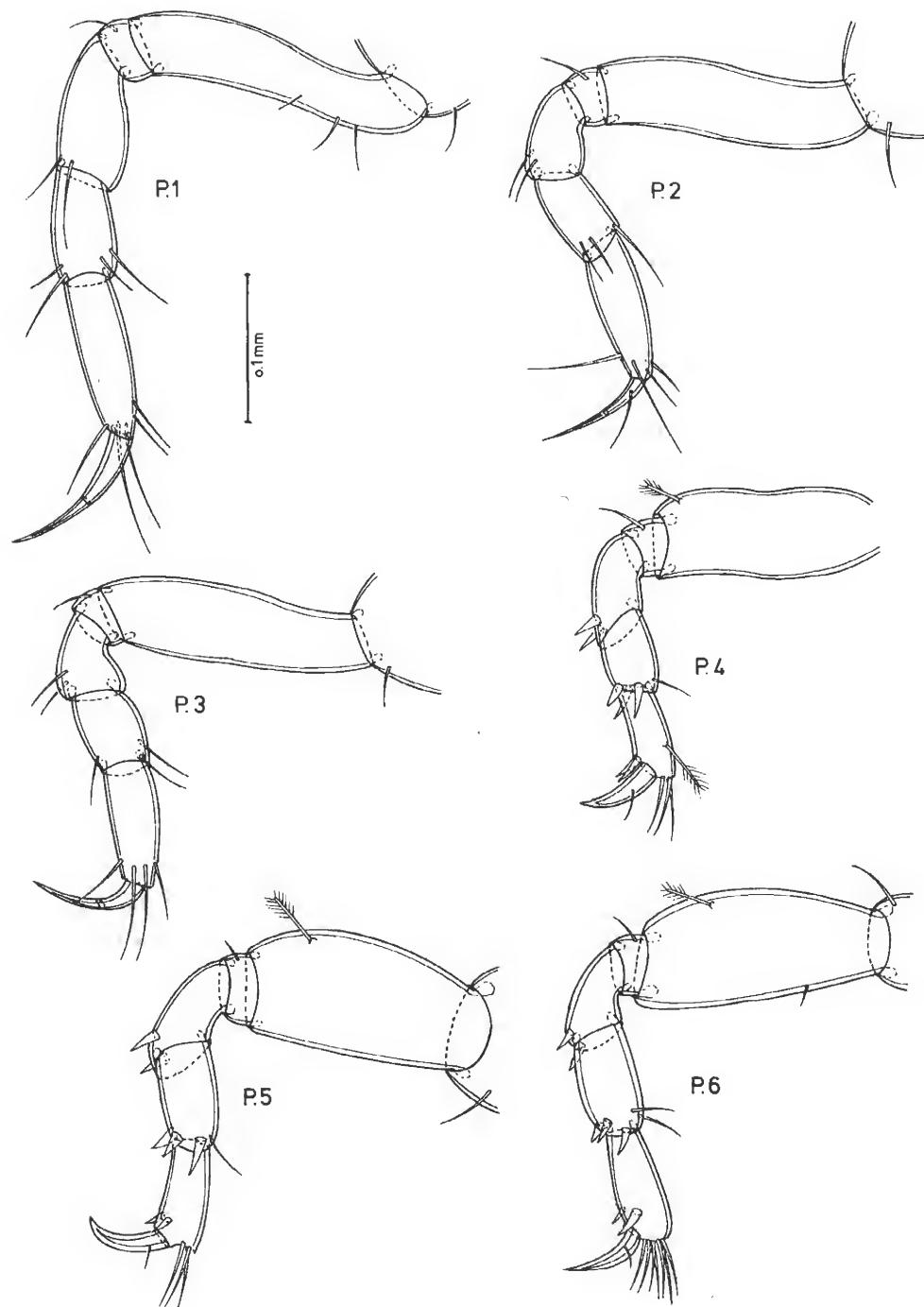


Figure 3. *Teleotanais gerlachi* (female). P 1–6 = pereopods 1–6.

The specimens examined also show a color pattern to distinguish them from *Paratanais*. Populations of *Teleotanais gerlachi* from both Crystal River, Florida, and from Port Hartcourt, Nigeria, have more or less dark brown spots of pigment all over the body (Figure 1), quite similar to those occurring on the tanaid genus *Zeuxo* Templeton, 1840. In comparison *Paratanais* normally has a yellow-white color, which sometimes grades into a more or less dark brown. At present we are not sure if this color pattern in our material of *T. gerlachi* is distinctive for the species, since the type-material, as well as preserved specimens from San Salvador are yellowish-white. The apparent lack of pigment may depend on the kind of fixation or preservation, which may have caused loss or dispersal of pigment over time. But it is also possible that different color patterns may occur among different populations of *T. gerlachi*. Intraspecific variation in pigment pattern is known for members of the family Tanaidae and has been studied extensively in *Parasinelobus* (=*Tanais*) *chevreuxi* (Dollfus, 1898) by Cléret (1966).

Distribution — Presently *T. gerlachi* is known from so few and such widely separated localities that we cannot make any meaningful observations on its distribution pattern. The type-material was recorded by Lang (1956) from the

coast of Brazil near Santos and at Cananéia. Additional material was reported by Sieg (1976) from the coast of El Salvador between La Libertad and San Diego and from La Herradura. It should be noted that records of *T. gerlachi* from the Atlantic and Pacific coasts of Panama Canal Zone (Sieg 1976: 83) were the results of misidentifications.

Ecological Remarks — *Teleotanais gerlachi* seems to occur intertidally in euryhaline habitats. All records are from the upper littoral and species occurring there must be able to tolerate a wide range of salinities; therefore, it is not surprising that the specimens collected between La Libertad and San Diego in El Salvador were from a freshwater pool. This species may have a preference for mangrove habitats (e.g., Cananéia) as is known for the euryhaline tanaid *Sinelobus stanfordi*. An indication for this might be seen in the co-existence of both species at Cananéia and Port Hartcourt (see Material Examined, Lang 1956).

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Taxonomy and Distribution of *Edotea* (= *Tropedotea*) *lyonsi* (Menzies and Kruczynski, 1983) N. Comb. (Crustacea: Isopoda: Idoteidae)

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SHORT COMMUNICATIONS

TAXONOMY AND DISTRIBUTION OF *EDOTEA* (= *TROPEDOTEA*) *LYONSI* (MENZIES AND KRUCZYNSKI, 1983) N. COMB. (CRUSTACEA: ISOPODA: IDOTEIDAE)

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ABSTRACT *Tropedotea lyonsi* Menzies and Kruczynski, 1983, is reported from the waters off Alabama southeastward to Cape Romano, Florida. The monotypic genus *Tropedotea* was recently erected on the basis of coxal plates of pereonites V to VII visible in dorsal view and a reduced number of articles in both antennae. Pereonites V to VIII are also visible in dorsal view in *Edotea* Guérin-Ménéville, 1843, and the number of articles in antenna 1 and 2 of *Tropedotea* Menzies and Kruczynski, 1983, is the same as in *Edotea*. Hence *Tropedotea lyonsi* is assigned to the genus *Edotea* and *Tropedotea* is designated a junior synonym of *Edotea*.

A total of 40 individuals of *Tropedotea lyonsi* Menzies and Kruczynski, 1983, were collected with a box core from 12 stations (Figure 1) during the Outer Continental Shelf studies of the Minerals Management Service (formerly the Bureau of Land Management) along the west coast of Florida and in the northern Gulf. The monotypic genus *Tropedotea* Menzies and Kruczynski, 1983, was distinguished from *Edotea* Guérin-Ménéville, 1843, by having coxal plates visible in dorsal view, antenna 1 consisting of 4 articles and antenna 2 with 5 articles. The remaining characters listed for the genus (e.g., pleon of 2 partly fused segments, maxilliped triarticulate, pereopods 1-7 subsimilar, etc.) are not unique but characteristic of other genera of the family Idoteidae as a whole.

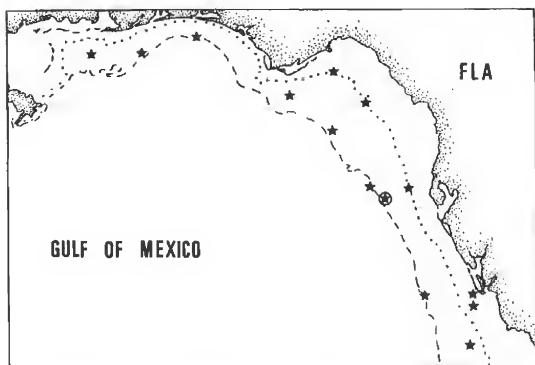


Figure 1. Distribution of *Edotea* (= *Tropedotea*) *lyonsi* in the eastern Gulf of Mexico. Circled star is type locality. Depth contours are 20 and 40 meters.

Edotea is diagnosed as having coxal plates not visible in dorsal view (Richardson 1905, p. 394, Menzies and Frankenberg 1966, p. 21). *Tropedotea lyonsi* has coxal plates visible in dorsal view, although they are difficult to distinguish. This character is not unique to the genus *Tropedotea* and until now has been apparently overlooked in the genus *Edotea*. *Edotea triloba* (Say, 1818) (= *E. montosa* Stimpson, 1853) from the northern Gulf of Mexico, from the coast of Georgia, and from Newport, Rhode Island, have indications of the coxal plates on pereonites V to VII in dorsal view, incompletely fused with pereonites V to VII. Under sufficient magnification, the remnants of the articulation may be seen, the imperfect fusion evident in both juveniles and adults. The generic diagnosis of *Edotea* should be emended to state coxal plates imperfectly fused to pereonites V to VII and partly visible in dorsal view.

The second distinctive feature given by Menzies and Kruczynski for the genus *Tropedotea* was the number of antennal articles, 4 in antenna 1 and 5 in antenna 2; however, the basal article of antenna 1 and the minute 6th article on antenna 2 were overlooked in the original description of *T. lyonsi*. An examination of the paratype has shown the antennae of *T. lyonsi* to be in agreement with *Edotea* in the number of articles of both antennae. Dr. T. E. Bowman (U. S. National Museum of Natural History, *in litt.*) has confirmed our observations on the type-specimen.

As noted previously, the remaining characters described for the genus *Tropedotea* are shared by other genera within the family Idoteidae. We consider the bilobed frontal lamina of the cephalon and the presence of a pair of bifid spines on the carpus of each pereopod of *T. lyonsi* as specific rather than generic characters. For the above reasons we assign *Tropedotea lyonsi* Menzies and Kruczynski, 1983, to the genus *Edotea* Guérin-Ménéville, 1843, and consider *Tropedotea* Menzies and Kruczynski, 1983, a junior synonym of *Edotea*.

Edotea lyonsi (Menzies and Kruczynski, 1983);
new combination.

Tropedotea lyonsi Menzies and Kruczynski, 1983, p. 10,
figure 3.

Material Examined — 1 ♀, PARATYPE, 14 November 1967, dredge, 26°24'N, 82°28'W, 18 m. USNM 204998, 1 ♂, 4 ♀♀, July 1976; 1 ♂, 1 ♀, September 1977, 29°54'N, 87°24'W, 27 m, fine sand. 1 ♂, June 1975, 29°33'N, 87°24'W, 83 m, coarse sand. 1 ♀, September 1977, 30°08'N, 86°30'W, 40 m, medium sand. 5 ♀♀, June 1975, 29°12'N, 85°00'W, 28 m, medium sand. 1 ♂, July 1976, 29°36'N, 84°18'W, 19 m, silty fine sand. 3 ♀♀, June 1975; 1 ♀, July 1976, 29°01'N, 83°45'W, 21 m, medium sand. 1 ♂, 1 ♀, August 1977, 28°42'N, 84°18'W, 37 m, silty fine sand. 2 ♀♀, June 1975, 27°59'N, 83°42'W, 36 m, silty fine sand. 2 ♀♀, July 1976, 27°59'N, 83°08'W, 17 m, very fine sand. 7 ♂♂, 3 ♀♀, September 1977, 26°25'N, 82°59'W, 39 m, fine sand. GCRL 1119, 1 ♀, May 1975; GCRL 1120, 1 ♀, September 1977, 26°25'N, 82°15'W, 10 m, very fine sand. 1 ♀, September 1977; 2 ♀♀, November 1977, 26°45'N, 82°20'W, 26 m, fine sand (Invertebrate Section Collection, GCRL).

Diagnosis — Cephalon twice as wide as long, frontal lamina bilobate, visible in dorsal view; dorsal crest of cephalon bilobate, acutely raised; antenna 1 with 5 articles, last minute (Figure 2C), antenna 2 with 6 articles, last minute; pereopods 1 to 7 with 2 bifid spines on carpus; lateral margins of pereonites 1, 5, 6, and 7 rounded, lateral margins of pereonites 2, 3, and 4 angular and somewhat bilobate, dorsal boss of pleosome low, little indication of fusion in pleosomal segments; appendix masculina with single row of transverse spines, about 8 in number (Figure 2A, B).

A great deal of variation is present within *Edotea triloba* and has led to taxonomic confusion. Many workers still

recognize *E. montosa* Stimpson, 1853, and *E. acuta* Richardson, 1900, as valid taxa. This is despite the work of Wallace (1915, p. 24) who reported the variation of *E. triloba* (Say, 1818) is extensive. He synonymized the above three names, stating "there appears to be, therefore, no good reason for separating *E. montosa* and *E. acuta* from *E. triloba*" (p. 26). Dr. T. E. Bowman has indicated his agreement with Wallace's conclusion (*in litt.*).

We examined our specimens of *Edotea lyonsi* to document possible intraspecific variation. No marked variation was found among the specimens during this study. Minor differences in the shapes of the frontal lamina of the cephalon and the lateral margins of the pereonites from the original description were attributable to sexual dimorphism or to growth stages. No significant variation was noted in these or the development of the dorsal boss of the pleosome.

Comparison of the appendix masculina of male *E. lyonsi* with published illustrations of that of *E. montosa* (Menzies and Frankenberg, 1966, Figure 2f) and with specimens of *E. triloba* from both Atlantic and Gulf populations has shown several discrepancies that may be of diagnostic value. A difference was noted in the presence of fewer spines on *E. lyonsi* than in *E. triloba*. The apex of the appendix masculina also reaches far beyond the endopod in *E. lyonsi* and only slightly beyond in *E. triloba*.

Little ecological or distributional information is available for *E. lyonsi* since the type material was based on only two specimens from a single collecting site in 18 m of water off Tampa Bay, Florida. Our collection data indicate that *Edotea lyonsi* is most common in marine waters from 10 to 40 meters deep on fine to medium sand substrata having high carbonate content. Associated species included the amphipods *Acanthohaustorius* sp.; *Eudevenopus honduranus* Thomas and Barnard, 1983; *Metharpinia floridana* (Shoemaker, 1933); *Ampelisca bicarinata* Goeke and Heard, 1983; and the shrimp *Leptochela papulata* Chace, 1976. These taxa are typically sand-dwelling species and support the observation *E. lyonsi* is common on sand bottoms.

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The authors wish to thank Thomas E. Bowman (National Museum of Natural History) for his examination of the holotype of *Edotea lyonsi* and his comments on the manuscript. David K. Camp (Florida Department of Natural Resources) also made valuable comments on the manuscript and loaned us the paratype of *E. lyonsi* for study. The specimens (other than the type material) used in this study were collected under Bureau of Land Management contracts to the State University System of Florida Institute of Oceanography (contract 08550-CT-11) and to Dames and Moore (contract AA550-CT7-34) during a baseline study of the continental shelf of the eastern Gulf of Mexico.

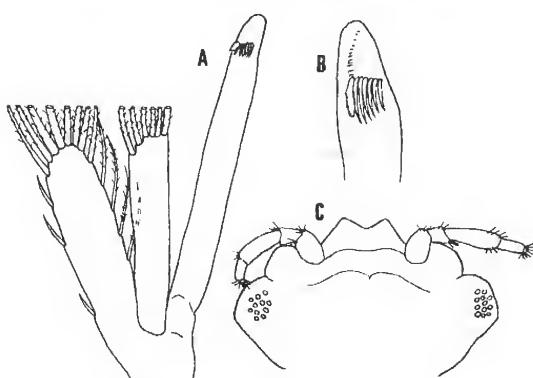


Figure 2. *Edotea* (=*Tropedotea*) *lyonsi*. A) pleopod 2 of male, B) detail of appendix masculina, C) frontal margin of cephalon (paratype).

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A Historical Note Concerning Salt in Vertebrate Blood and in the Sea

Gordon Gunter

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A HISTORICAL NOTE CONCERNING SALT IN VERTEBRATE BLOOD AND IN THE SEA

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ABSTRACT In 1902 and 1903 G. von Bunge and A. B. Macallum became impressed independently with the similarity between the salt content of ocean water and vertebrate blood. Von Bunge's ideas concerned NaCl and were stated in a physiology text. Macallum's ideas, related mostly to the proportions of Na, K, and Ca in sea water and blood, were set forth in a series of papers ending in 1926. Bayliss (1927) and Pearse and Gunter (1957) accepted this thesis. Conway (1943, 1945) questioned it on the grounds that the salts from land erosion do not correspond to those in the sea. However, Rubey (1951) has shown that sea salt has come from the deep Earth rather than erosion. All ensuing discoveries have corresponded to that idea. As a side issue, the theory of the freshwater origin of fishes has succumbed to a large number of questioning papers. Now the von Bunge-Macallum theory is generally unquestioned.

Some 81 years ago a German professor named Gustav von Bunge first sensed the importance of salt in the sea and in vertebrate blood, including the fluids of men and other mammals. He stated this idea in the fourth edition of his *Lehrbuch der physiologischen und pathologischen chemie*.

The fourth edition of the physiological chemistry text by von Bunge was translated by Florence A. Sieveking Starling and edited by her famous husband and published in this country as a *Textbook of Physiological and Pathological Chemistry* by Bunge (1902), P. Blakiston's Son and Co., Philadelphia. In England the same book was published by Kegan Paul. Presumably the fourth German edition was published in the same year, although I have not seen it.

The attention of von Bunge seems to have been centered upon salt alone, which in the language of his day meant NaCl. Further developments led to more complicated ideas, but von Bunge's thoughts seem to have been the beginning of the salinity picture of blood today as it involves physiology.

Von Bunge drew many sentient conclusions about the kidneys, the blood of vertebrates, and the distribution of salts of the alkaline earth metals sodium and postassium. He pointed out that the carnivores and meat-eating men did not crave salt (NaCl) but that plant-eaters in animal populations and human society were always craving it. He said people probably overloaded their kidneys and caused nephritis by taking too much salt. This admonishment has a distinctly modern ring, but today the reasons are stated somewhat differently, although von Bunge may have been very close to correct for it is now known that the kidneys have as much to do with high blood pressure as the heart does, or more.

Von Bunge called attention to the fact that vertebrate fluids are replete with NaCl, but plant tissues are potassium dominated. Thus the herbivores are always seeking salt (NaCl) for their blood and other fluids.

Von Bunge said on page 101 of this treatise, "I am, however, convinced that the remarkably high percentage of salt in vertebrate animals, as well as the desire to take salt with our food, can only be satisfactorily explained by the theory of evolution." That was a sharp insight due to his predilection for speculative thinking with the evidence available to him.

He noted that most plants are rich in potassium and poor in sodium, except for marine species, and that the invertebrate land animals are similar to typical land plants in salt content. In summary, he said (p. 103), "These are facts which lead most readily to the interpretation that the vertebrates living on dry land originally came from the sea, and are still continuing to adapt themselves to their present surroundings, where they can get but little salt." Von Bunge's theory was a great leap forward and had great effect as the sudden truth always does. Von Bunge (1902) said that he was advancing his theory for the first time.

There is a certain anomaly in the dating of von Bunge's publications which I have not resolved at this writing. I have not seen a fourth German edition of his *Lehrbuch*, etc. of which the 1894 edition is said to be the "Dritte Aufl." The situation is compounded by the listing of the American edition (P. Blakiston's Son and Company) of the English edition as the "Second English Edition." I know of no first English edition unless the London edition by Kegal Paul of the same date, a facsimile reproduction so far as I can see, is termed a first edition. This would be a bit odd and cavalier, but no more so than the English custom of ignoring hereditary titles such as the von of von Bunge, for everyone except the British. However, precise priority is not of deep importance and ideas may come from diverse workers at close periods or discoveries may come independently from various workers at closely related times.

A. B. Macallum at Johns Hopkins University was led to somewhat similar conclusions as those of von Bunge by a different approach. He first considered the salt ions in marine medusae (1903) and later considered the differences

between animal and plant fluids as related to paleochemistry (1904) with a later treatment of vertebrates and invertebrates (1910). A summary of the whole question was reviewed by Macallum (1926). Macallum seems to have been more experimental than von Bunge, but his facts are no more trenchant or correct. Thus the whole situation seems to be an excellent example of how important new ideas spring at quite close times out of the *zeitgeist*.

Macallum seems to have been drawn to his conclusions by the similarity between the proportions of sodium, calcium, and potassium in blood and sea water. Lower concentrations in blood were explained by the great time elapsed since vertebrates left the sea. These reasons apparently satisfied Bayliss (1927) who quoted them on page 210. He added that sea water is a good physiological solution when diluted to the same osmotic pressure as the blood, although "the amount of magnesium is unnecessarily great." The same could be said of sulphate.

In the deep ocean where warm sea water has been found welling up from the magma in areas near the margins of the deep Earth plates a rich fauna has been found. Recent work has shown that little oxygen is available but there is an oxidation system depending on sulphate in the upwelling water.

The von Bunge-Macallum theory of the connection between sea water and vertebrate blood has been widely accepted and, therefore, not commented upon very much. Rogers (1927) presented the theory concerning marine origins in succinct terms:

The first living organisms had the sea for their environment. Every cell doubtless came into contact with this fluid which was at the same time the source of its food and oxygen supply. As cells began to be associated in smaller or larger masses, channels were left between them through which the water of the sea might find passage. Animals a little further along the scale of development shut off their body cavities, vascular and otherwise, from direct communication with the sea, but did not succeed in freeing the cells from

the necessity of getting their food and oxygen supplies from a solution. The fluid shut within the animal body furnished the immediate environment of the cells; it took the place of the sea in the environment of the organism. It has been seen that the fluid becomes more and more complex as one passes in review from lower to higher forms. And while the internal fluid sea, bathing the individual cells, has become more complex and able to play a greater variety of functions in the life of organisms, there are certain features in which it harks back to the primitive conditions which must have existed millions of years ago.

The only serious demurra was advanced by Conway (1943, 1945) in two important papers showing the components of salt in the sea that have resulted from weathering and land drainage. He found poor correspondence between the components of land drainage and the salinity of the sea and that was accepted by some people as disproving the theory of blood connection with the sea. Actually there is no logical connection between the real origin of sea salt and the components of salt of mammalian blood. The important fact is correspondence or similarity which came about after the sea salt proportions were established.

In any case, it was shown later by Rubey (1951) that sea water comes chiefly from the magma and the deep earth and not from the atmospheric halogens. There has been no real dispute of Rubey's conclusions.

In 1957 Pearse and Gunter reviewed this question in a chapter on salinity and gave their adherence to the von Bunge-Macallum thesis. Since then nothing has transpired except that the theory of the freshwater origin of fishes has finally been laid to rest and rejected by a long series of papers which have disproved it on all points. All in all it is a side issue and will not be treated here. The chief modern protagonist of freshwater origin, A. S. Romer of Harvard, never gave up during his life, but to no avail so far as continuance of the theory was concerned. Today there are no adherents remaining, at least not any who wield the pen. And so the theory of marine origin of vertebrates and their blood now remains unquestioned.

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A Note on the Reproductive Season of the Carolina Marsh Clam *Polymesoda caroliniana* (Bosc) in an Irregularly Flooded Mississippi Marsh

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A NOTE ON THE REPRODUCTIVE SEASON OF THE CAROLINA MARSH CLAM *POLYMESODA CAROLINIANA* (BOSC) IN AN IRREGULARLY FLOODED MISSISSIPPI MARSH

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ABSTRACT The gonadal development of *Polymesoda caroliniana* in an irregularly flooded, brackish marsh was followed for 13 months. Ripe individuals (condition prior to spawning) were found in May, July, August, and October, suggesting either an extended period of spawning or three discrete spawning periods. This pattern is different from another study of *P. caroliniana* in a more flooded habitat.

The observed gonadal condition correlates with the presence of newly recruited clams in the marsh during most of the year, but failed to explain a pulse of juveniles found in February. The different reproductive pattern observed in this brackish marsh may be either a genetic or physiological adaptation to life in an unpredictably flooded marsh.

INTRODUCTION

The Carolina marsh clam *Polymesoda caroliniana* (Bosc 1802) is a moderate-sized clam, 25–40 mm, and occurs from Virginia to Texas. Present systematics place *P. caroliniana* in the family Corbiculidae which primarily includes fresh and brackish water bivalves. The clam is found in shallow water or intertidal habitats (Van der Schalie 1933, Tabb and Manning 1961, Hoese 1973, Swingle and Bland 1974, Olsen 1976, Subrahmanyam et al. 1976, Duobinis 1978, Duobinis-Gray and Hackney 1982).

Only Olsen (1976) provided information on the reproduction of *P. caroliniana*. He examined the reproductive cycle of a population on the northwest Florida Gulf coast and found that it spawned from July through September. Little is known about the physical conditions necessary to induce spawning. Olsen (1976) suggested that a 5-ppt change of salinity would induce spawning. Tabb and Moore (1971), however, suggested that reproduction occurs at salinities under 5 ppt and is most successful in fresh water. Conversely, Cain (1973) believed that the larvae were killed in salinities below 2 ppt and needed at least 6 ppt to remain viable.

Two studies of the fauna of a high intertidal, low-salinity marsh in Mississippi found newly recruited specimens of *P. caroliniana* present during much of the year (Bishop 1981, Duobinis-Gray and Hackney 1982). These recruitment patterns did not fit the spawning patterns found by Olsen (1976) in a northwest Florida population. Two hypotheses might explain this discrepancy: 1) the Mississippi population had a different spawning season, or 2) the larvae of *P. caroliniana* were capable of long-term residence as meroplankton, i.e., they delayed metamorphosis. The following study of the reproductive condition of *P. caroliniana* in an irregularly flooded Mississippi marsh over a 13-month period: 1) examines whether clams in this stressed habitat produce gametes,

and 2) determines whether reproduction by clams in the intertidal population could explain the recruitment patterns previously noted.

MATERIALS AND METHODS

Study Area

The tidal marshes on the western side of St. Louis Bay, Mississippi ($30^{\circ}22'N, 89^{\circ}15'W$), are well studied (Hackney and de la Cruz 1982). They are irregularly flooded and dominated by the black needlerush *Juncus roemerianus* (Schlee). The sediment in the top 10 cm of the marsh is approximately 36% sand, 18% silt, and 46% clay (Bishop 1981) and the salinity of the flooding water has only occasionally exceeded 8 ppt (Hackney and de la Cruz 1982).

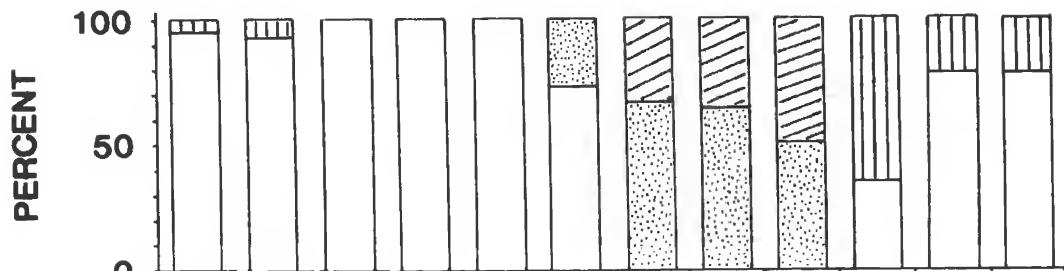
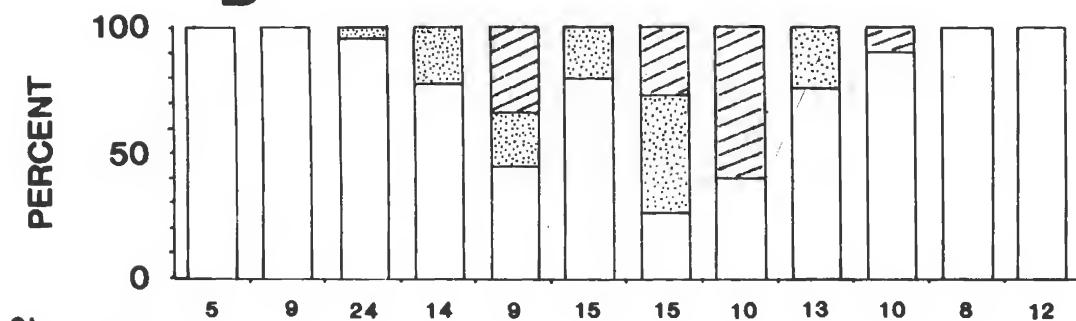
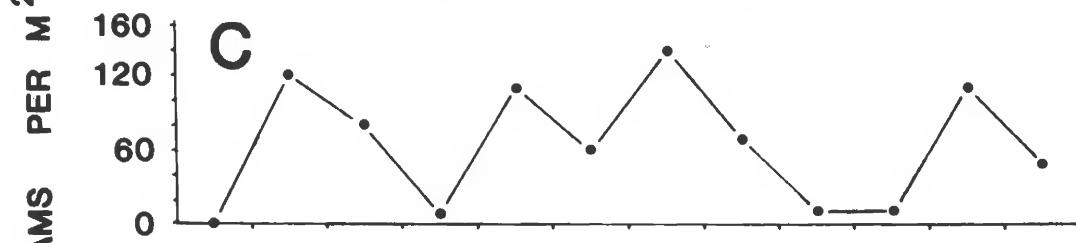
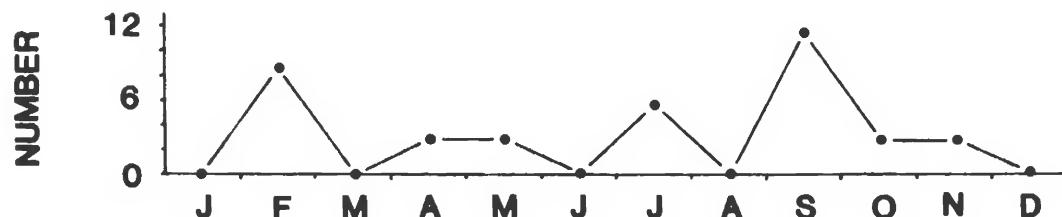
Gonadal Study

Clams were collected monthly from March 1979 through March 1980. Approximately 20 individuals were collected each month, but some were later determined to be unsuitable or regarded as subadult (< 20 mm) and not used. Each clam was fixed, embedded in parafin and sectioned (8 μm). Sections were taken from portions of the entire gonadal area, stained with hematoxylin and counterstained with eosin. The designation of gonadal condition followed Olsen (1976) who graciously loaned photographs of each reproductive stage to insure consistency between the two studies. Those interested in detailed aspects of gametogenesis in *P. caroliniana* should refer to Olsen (1976).

RESULTS AND DISCUSSION

Ripe individuals (male and female) were found in May, July, August, and October (Figure 1) in the Mississippi marsh. This extends the potential spawning season two months earlier and one month later than Olsen's (1976) study in Florida (Figure 1A). Curiously, there were no ripe individuals in June or September. All clams collected in November, December, January, and February showed no gonadal

EARLY ACTIVE
& SPENT LATE ACTIVE RIPE PARTIALLY SPENT

A**B****C****D**

development (Figure 1B). This contrasts with Olsen's (1976) study in which a significant proportion of clams from October through February were partially spent (condition following spawning), a condition that was never noted in this study. Furthermore, from July through September all individuals in the Florida population were either in the late active stage of development or ripe. This was never the case in the Mississippi population (Figure 1B). While these data suggest that the Mississippi population has three spawning periods; May, July-August, and October, a more thorough study with shorter intervals between collections and more individual clams would be needed to substantiate such a claim.

The reproductive pattern found in the Mississippi population explains the occurrence of very small specimens of *P. caroliniana* in late spring and early summer (Figure 1C), the pulse of juveniles in September (Figure 1D), and the pulse in November (Figure 1C). The February pulse that was reported by Bishop (1981) and Duobinis-Gray and Hackney (1982) cannot be explained without either assuming a lengthy planktonic period or the spawning of another nearby population at a different time. The data used in Figure 1C and 1D were collected during different years, but the gonadal data (Figure 1B) and the recruitment data (Figure 1D) overlapped except for April and May.

Survival in a high, intertidal marsh is difficult for animals that depend on the flooding tide for food and reproduction. Even though *P. caroliniana* can survive for weeks without water (Duobinis-Gray and Hackney 1982) it is undoubtedly stressed by long periods without inundation. Such conditions frequently occur in this marsh (Hackney and de la Cruz 1982). In addition to testing the physiological tolerance of these clams, the lack of inundation prevents the release of eggs and sperm and the settlement of larval clams. It is not surprising that different degrees of recruitment would be noted for the same area from year to year, both in timing and abundance (Figures 1C & 1D).

The extension of the reproductive season in the Mississippi intertidal population is a response that would aid suc-

cessful reproduction. If reproductive effort was restricted to a single spawning period, the entire year's effort would be wasted if the marsh did not flood. By extending the reproductive period, some degree of success is insured each year. Furthermore, these data suggest that at least a portion of the population is spawning twice because the sum of clams spawning over a year equals 129% of the population.

Variations in timing of gonadal maturity between Florida and Mississippi populations may be genetically based or the result of external forces acting upon a population which is physiologically plastic. For instance, both populations may be responding to the same external stimulus, e.g., temperature. If temperature was the primary factor controlling gonadal development, then variations between populations could be explained without the presumption of genetic differences. The intertidal population would reach the critical spawning temperature earlier than a more flooded population because it lacks the protective insulation of the water. Thus, the difference in timing of gonadal activity does not necessarily mean that Florida and Mississippi populations are different physiological races.

CONCLUSIONS

Carolina marsh clams inhabiting a relatively high intertidal marsh produced mature gametes indicating that poorly flooded populations are reproductively viable. Variations in gonadal development were found between well flooded and irregularly flooded intertidal populations of *P. caroliniana* living at the same latitude. Whether the populations differ genetically or are exhibiting physiological plasticity is unknown. Recruitment of juveniles during the year cannot be explained entirely by the reproductive pattern of adults or by the intertidal habitat prior to the recruitment period.

ACKNOWLEDGMENTS

The author thanks Lawrence Olsen for the unrestricted use of photographs depicting gonadal development and T. Dale Bishop for the free use of unpublished data.

Figure 1A. Reproductive state of adult clams (> 20 mm) from a subtidal area in the Ochlockonee River estuary on the northwest Florida coast (modified from Olsen 1976). Each collection datum represents 20 clams collected from November 1974 through October 1975. B. Reproductive state of adult clams (> 20 mm) from a high intertidal marsh in Mississippi. The number below the month indicates the number of clams examined. Collections were made from March 1979 through March 1980. March on the figure includes clams collected in March 1979 and March 1980. C. Recruitment of juvenile clams (2.5–4.0 mm) into a high intertidal marsh in Mississippi (adapted from Duobinis 1978). Data were collected from February 1977 through January 1978. D. Recruitment of juvenile clams (< 4.9 mm) into a high intertidal marsh in Mississippi (data provided by T. D. Bishop, Dept. Ecology, Univ. Georgia, Athens, GA). Data were collected from June 1979 through May 1980.

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Size and Distribution of Resting Eggs in a Natural Population of the Rotifer *Brachionus plicatilis*

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SIZE AND DISTRIBUTION OF RESTING EGGS IN A NATURAL POPULATION OF THE ROTIFER *BRACHIONUS PLICATILIS*

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ABSTRACT Resting eggs of the rotifer *Brachionus plicatilis* were collected from the sediments of a brackish-water pond near Tampa, Florida. These core samples were examined for resting egg density and size. Resting egg density decreased exponentially from the surface down to 7 cm in the sediments at all stations, with depth in the sediments accounting for 42.3% of the total variance. The maximum resting egg density recorded was 194 RE/cm³ with no significant differences in density among stations. Resting eggs were found to be significantly larger in the top 2 cm of sediment than resting eggs from deeper in the sediments. These data are discussed with regard to other work on resting egg densities in natural populations. Hypotheses are offered to explain the observed decrease in resting egg size with depth in sediments.

INTRODUCTION

The life cycle of monogonont rotifers is one of cyclical parthenogenesis (Birky and Gilbert 1971), with sexual reproduction occurring intermittently in response to specific environmental cues (Gilbert 1977, Pourriot and Rougier 1979, Pourriot and Clement 1981). The products of sexual reproduction are resting eggs which have a resistant outer shell and are capable of remaining dormant for up to several years (Gilbert 1974, Pourriot and Snell 1983). Resting eggs are energetically costly to make and, as a result, females producing resting eggs exhibit low net fecundity (Gilbert 1980). However, because of their capacity for extended dormancy, it is theoretically possible for resting eggs to accumulate in the sediments over several years reaching quite high densities.

The few reports on resting egg densities in natural populations (Ito 1958, Nipkow 1961) have suggested that resting eggs may indeed be present in the sediments of lakes and ponds in substantial quantities. As a result, we decided to investigate the density and distribution of resting eggs of the brackish-water rotifer *Brachionus plicatilis* in a pond known to support large and persistent adult populations. Secondly, we have examined resting egg size and its variation with resting egg distribution.

MATERIALS AND METHODS

Resting eggs of the brackish-water rotifer *Brachionus plicatilis* were collected from the bottom sediments of a small, brackish-water pond (Westshore Pond), in Tampa, Florida. This approximately 100-m-diameter pond is connected to Tampa Bay by a narrow canal about 1 km long. The pond exhibited small tidal fluctuations and ranged from 10 ppt to 28 ppt in salinity and from 10°C to 33°C in temperature throughout the year. The sediments consisted primarily of mud rich in organic material and detritus. Because Westshore is a small pond, the sediment was rather homogeneous throughout, without any noticeable differences

between stations.

Ten-cm-diameter bottom cores were taken from five stations at various sites around the pond. From each core sample, three replicate subcores, 1.5-cm-diameter by 7-cm-deep, were removed for analysis. Each subcore was then sliced into 1-cm sections, according to depth, and the resulting 1.5-cm by 1-cm sections were filtered through a sieve series of 1024-μ, 512-μ, 256-μ, 128-μ, and 64-μ mesh. To determine resting egg density, the residue on the 64-μ sieve was washed into a small beaker with 25 ml of 1.75-M sucrose solution. This was followed by a second wash with 5 additional ml sucrose. The mixture of residue and sucrose solution was then poured into 1-ml counting chambers and the resting eggs were counted at 25X magnification under a stereomicroscope.

One of the major difficulties in counting resting eggs is separating them from debris in the sediments. Because they are small (110 × 70 μ), resting eggs are easily obscured by sand grains and other particles. The use of a high molarity sucrose solution causes resting eggs to float and facilitates more accurate counting. Utilizing the sugar flotation technique, we were able to recover substantially more resting eggs from the sediments than by sieve series filtration alone.

Resting eggs used for size measurements were not collected by sugar flotation. All eggs used for size determination were only filtered through a sieve series and then washed from the 64 μ mesh filter with a 22 ppt salinity solution, the same salinity prevailing at the time of their collection from Westshore Pond. At least ten eggs were collected from each of the seven 1.5 × 1-cm sections, which were categorized according to depth. This was repeated for each of the three replicate subcores at Station C. In addition, eggs were also collected by filtration from the top 2 cm of the three replicate subcores of the other four stations. This permitted us to investigate resting egg size variability with depth at Station C as well as spatial variability in size among all stations in the top 2 cm of sediment. The length and width of each egg was measured with an ocular micrometer at 50X magnification with a Wild M5A stereomicroscope.

RESULTS

The highest resting egg densities were observed in the top 1 cm of sediment (Figure 1), with the maximum being 356 ± 50.4 /section ($194/\text{cm}^3$) at Station E. From the top 1 cm, resting egg density decreased exponentially with depth, until finally, at some stations no resting eggs could be detected in the 7 cm deep section.

Spatial variation in resting egg density was also examined among stations. The mean density at a station ranged from 40.8 eggs/ cm^3 , including surface to 7 cm depth, to 10.4 eggs/ cm^3 . A two-way ANOVA (Sokal and Rohlf 1969, p. 315) was performed on these data to partition the variation into depth, station, and interaction effects. Depth as well as the depth \times station interaction make significant contributions to the variance ($P < .001$), however, station contributions are non-significant. An examination of the variance components (Sokal and Rohlf 1969, p. 317) reveals that depth accounts for 42.3%, station 4.7%, depth \times station interaction 44.1%, and error 8.9% of the total variance.

Resting egg size, in both length and width dimensions, was found to vary with depth in sediments (Figure 2). Resting eggs collected from the top 2 cm were approximately 10% longer and 14% wider than eggs collected deeper. The results of Duncan's Multiple Range Test (Steel and Torrie 1960, p. 107) show that only eggs collected from the top 2 cm are significantly longer than eggs collected deeper (Table 1). A similar pattern exists with egg width.

A one-way analysis of variance (Sokal and Rohlf 1969, p. 208) of resting egg size in the top 2 cm of sediment among the five stations reveals small, but significant spatial heterogeneity. The F-values obtained were 3.191 ($P < .05$) and 9.16 ($P < .005$) for length and width respectively. Among the five stations, mean resting egg length varied about 10% from 99 to 110 μ and mean width varied about 18% from 61 to 75 μ .

DISCUSSION

The resting egg densities we observed were similar to those reported by Ito (1958) and Nipkow (1961). Examining the sediments of 15 eel-culture ponds in Japan, Ito (1958) collected sediment samples to a depth of 5.5 cm. He reported densities of *Brachionus plicatilis* resting eggs as high as $9.66/\text{mm}^2$, with large variations between ponds. In contrast to our results, Ito found no consistent differences in resting egg density with depth in sediment. It should be recalled, however, that we used the sugar flotation technique to determine resting egg density, while Ito apparently simply picked resting eggs from the sediments. Ito also reported the interesting observation that resting egg densities in sediment surface samples were positively correlated with the population density of *B. plicatilis* in the summer of the preceding year.

Resting egg densities in sediments of eight planktonic rotifer species have been reported by Nipkow (1961). He

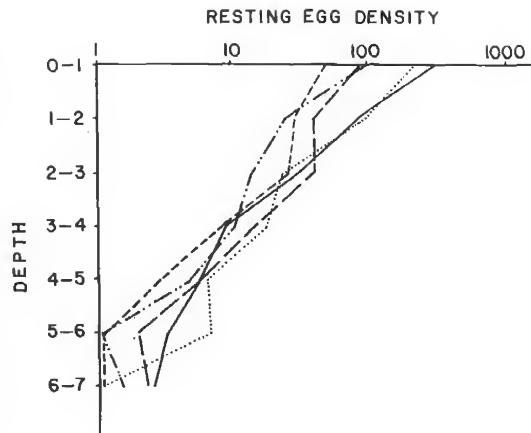


Figure 1. Resting egg density in sediments. Density is in resting eggs/section ($1.5\text{ cm diameter} \times 1\text{ cm deep}$), depth is in cm. Each of the five stations is represented by a different line.

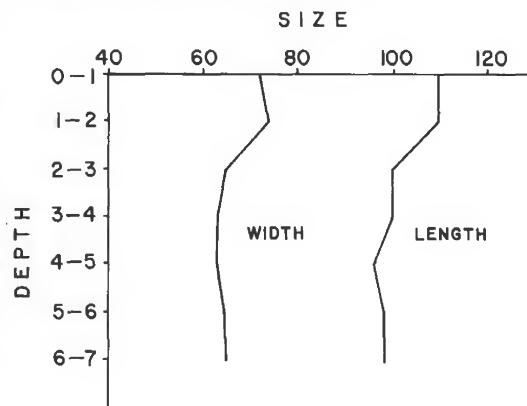


Figure 2. Resting egg size at various depths in sediments. Size is in microns, depth is in cm.

found surface sediment densities ranging from 1 to 6 resting eggs/ mm^2 for seven of the species, but densities between 30 and $40/\text{mm}^2$ for *Synchaeta oblonga*. When we convert our data on *B. plicatilis* resting egg densities in the surface sediments to similar units, we obtain maximum estimates of two resting eggs/ mm^2 . These results are similar to Nipkow's in spite of the fact that we used different collecting techniques.

Our observations, along with those cited above, clearly suggest that a rotifer resting egg pool in the sediments can be of substantial size. The existence of this pool acts as a buffer for rotifer populations during periods of environmental unsuitability. The resting egg pool provides a vehicle for rapid recolonization when conditions become favorable again for growth.

TABLE I.

Results of Duncan's Multiple Range Test on resting egg length and width. Table entries are the mean lengths and widths in microns at each depth.

		Length					
110	110	100	100	99	99	96	
Width							
74	71	65	64	64	63	63	

Species specificity in resting egg size has been recorded by several authors. Nipkow (1958) observed eggs collected from natural populations of *Brachionus calyciflorus* and *B. angularis* to be 144–160 x 88–104 μ and 80–96 x 60–64 μ , respectively. The most extensive comparison of resting egg dimensions has been provided by Nipkow (1961) who lists resting egg dimensions for 45 rotifer species. The range includes the smallest resting eggs, those produced by *Cephalodella exigua* at 38 x 40 μ to the largest—*Brachionus calyciflorus* at 144–160 x 88–104 μ . Similar dimensions for *B. calyciflorus* resting eggs were reported by Bogoslavsky (1963). Pourriot (1967) has reported considerably larger resting eggs in two species of rotifers cultured in the laboratory. He found very large resting eggs in *Notomata collaris*

(215 x 170 μ) as well as *Tetrasiphon hydrocora* (200 x 155 μ). Females in both these species are large, ranging up to 650 μ . Pourriot also reported the resting eggs of *Lindia torulosa* (120 x 90 μ) and *Platyias polyacanthus* (132 x 118 μ) to be somewhat smaller, but within the range reported by Nipkow (1961).

The *B. plicatilis* resting eggs that we collected from West-shore Pond were intermediate in size at 96–110 x 63–74 μ . We also found significantly smaller eggs 2 cm or more into the sediments. Why would resting eggs from deeper in the sediments be smaller? There are at least three hypotheses that could explain this observation. The first is that greater osmotic pressures may exist deeper in the sediments, causing shrinkage of the extraembryonic space usually present in resting eggs (Wurdak et al. 1978). A second alternative is that deeper eggs could be older and, as a result of their age, be smaller from partial metabolism of energy stores within the egg. A third alternative is that size-selective sorting of resting eggs could have occurred causing the larger, more buoyant eggs to be retained toward the sediment surface and smaller, denser eggs to penetrate deeper into the sediments. Distinguishing among these hypotheses will require further investigation of resting egg structure, physiology and interaction with the sediments.

ACKNOWLEDGMENTS

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Amphipods of the Family Ampeliscidae (Gammaridea). II. Notes on the Occurrence of
Ampelisca holmesi in the Northern Gulf of Mexico

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AMPHIPODS OF THE FAMILY AMPELISCIDAE (GAMMARIDEA). II. NOTES ON THE OCCURRENCE OF *AMPELISCA HOLMESI* IN THE NORTHERN GULF OF MEXICO

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ABSTRACT *Ampelisca holmesi* is reported herein from the grass beds behind the barrier islands of the northern Gulf of Mexico. Previous records are reviewed and the male of the species is described for the first time. The material agrees well with the original description and the recent redescription. Mouthparts for *A. holmesi* are described, illustrated, and compared with those of *A. verrilli* from the northeastern coast of the United States.

Ampelisca holmesi Pearse, 1908, was described from Ferguson's Pass, Oyster Bay, Florida (Pearse 1908). This area corresponds with a region now known on most maps as Espero Bay on the southwestern coast of Florida, just south of Charlotte Harbor. An additional record for this species from the Gulf of Mexico is Pearse (1912), who examined material collected by the ALBATROSS off the Mississippi Delta from 50 to 54 meters. Several records for this taxon exist from the eastern coast of the United States. Shoemaker (1933, p. 3) cited the material in the collections of the U. S. National Museum and reported the distribution of the species to be "from Rhode Island; Connecticut; Beaufort, North Carolina; Key West, Florida; and Sarasota Bay, Florida."

Material examined during this study included four individuals collected from the northeastern Gulf of Mexico: two adult females, 12–13 mm, J. M. Gathof, collector, 25 October 1976 – 30°14'N, 88°18'W; 1 adult male, 12 mm, G. D. Goeke, collector, 14 March 1983 – 30°15'N, 88°44'W; 1 adult female, 10 mm, GCRL 167–794, 27 October 1967, southern side of Little Deer Island, Mississippi, D. H. Farrell, collector. Two of the females were collected from *Diplantha wrightii* grass beds, 1 mile east of the northwestern tip of Dauphin Island, Alabama, in 1 meter, using a 12-cm-diameter, plunger-type marsh corer. The single male was collected from *D. wrightii* grass beds at the northwestern tip of Horn Island, Mississippi, in 1 meter, using a scallop dredge. Both sites were characterized by a medium-sand substrate with detrital grass fragments at the sediment-water interface. Many large, tube-dwelling polychaetes, *Diopatra cuprea*, were present at the Dauphin Island collection site.

Ampelisca holmesi is very closely related to *A. verrilli* Mills, 1967, and the nature of this sibling species pair has caused some confusion in the records for the distribution of the former species. Mills (1967) has indicated that some of the records are almost certainly based on specimens of *A.*

verrilli, but was unable to confirm his suspicions as the material examined by Shoemaker (1933) could not be located in the holdings of the National Museum. Mills also indicated that other records from the eastern coast should be assigned to *A. verrilli* (see Mills 1967 for synonymy of *A. verrilli*). Additional records for the distribution of *A. holmesi* are the north central Gulf of Mexico (Farrell 1970) and the southwestern coast of Cuba (Ortiz 1978).

Mills (1967) listed the differences between *A. holmesi* and the closely related *A. verrilli* and stated that increased collecting would probably show the species "to be two members of a species flock related in similar features of head and pereopod 5" (p. 639). This appears to be the situation, as collections from the eastern Gulf of Mexico have revealed the presence of three undescribed but closely related species which possess the same generalized head and leg shapes (Goeke and Heard, in preparation).

The mouthparts of ampeliscids often are of specific diagnostic value (Goeke, unpublished data). A careful comparison of the mouthparts of *A. holmesi* and *A. verrilli* from the type locality has shown only minor differences. In sibling species pairs, mouthparts generally agree very well in structure and such is the case herein. Minor differences in the setation on the mandibular palp, facial setae of the palp of maxilla 1 and the number of gill rakers may all be attributed to age or clinal variations within the species. While it is unfortunate that no substantive diagnostic features could be found in the mouthparts, it demonstrates well the close relationship between the two species.

Maxilliped (Figure 1H) — palp normal for the genus, without diagnostic features for the species; inner margin of outer plate armed with 10 chisel-shaped spines and 4 setal spines, each spine with accessory seta; inner plate with row of submarginal medial and terminal setae, terminal margin with 2 setal spines and 2 chisel-shaped teeth (Figure 1 I). Maxilla 1 (Figure 1G) palp with 2 segments, 3 outer marginal plumose setae, 5 terminal spines and approximately 14 simple facial setae; outer plate with 11 terminal spines, the

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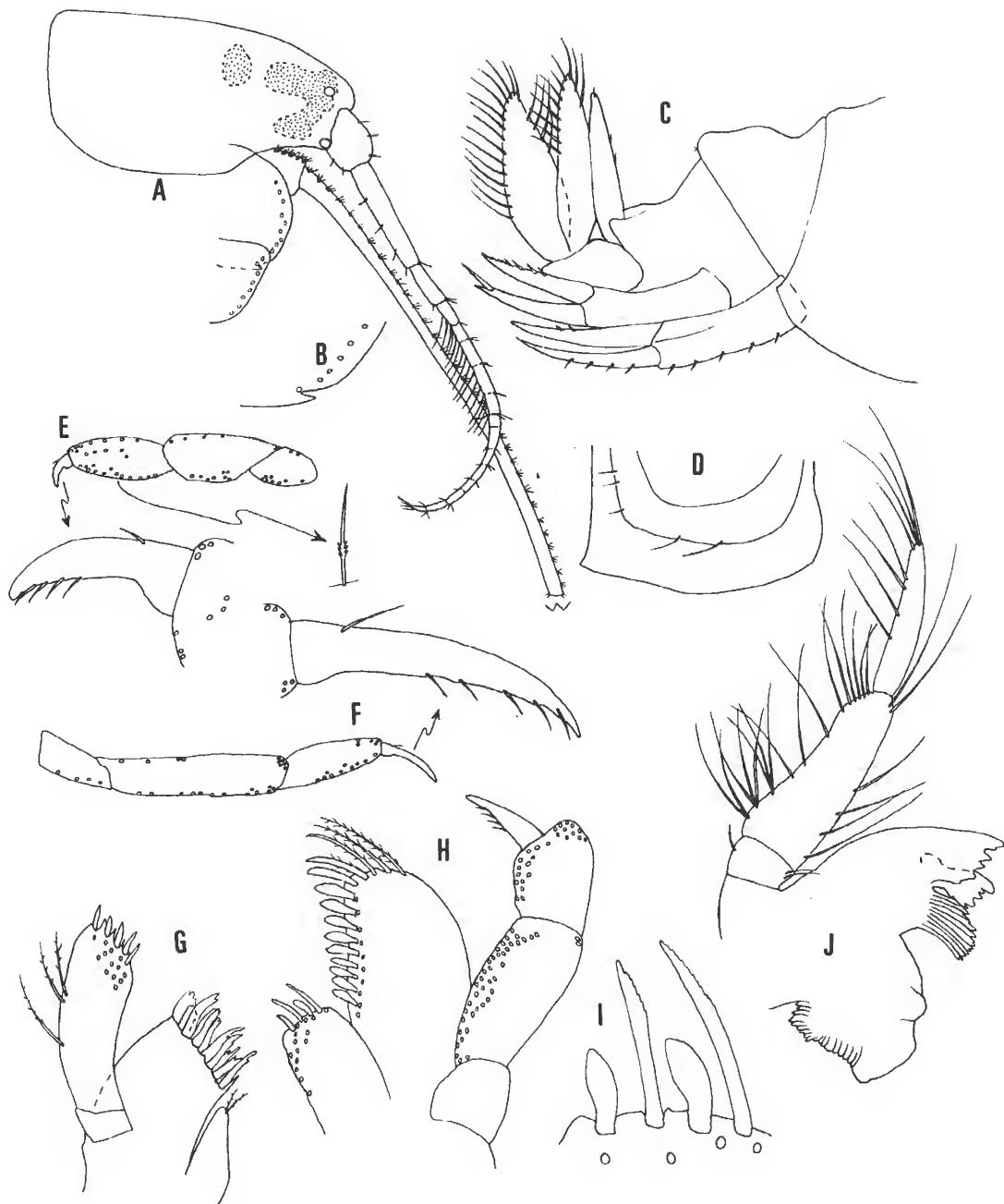


Figure 1. *Ampelisca holmesi*; A) head region, male; B) lower margin coxal plate 1, male; C) urosomite region, male; D) coxal plates 1–3, male; E) terminal segments of pereopod 1, male; F) terminal articles of pereopod 2, male; G) maxilla 1, female; H) maxilliped, female; I) detail of inner plate of maxilliped, female; J) mandible, female.

2 lateralmost spatulate; inner plate with 2 apical plumose setae. Maxilla 2, upper lip and lower lip all normal for the genus, without features of diagnostic value for the species. Mandible (Figure 1J) — palp with terminal article 4/5 length of penultimate article, latter article basally inflated; molar process with 5 teeth; lacinia mobilis with 6 teeth, 10 gill rakers.

The mature males of the genus *Ampelisca* quite often exhibit a high degree of sexual dimorphism and are usually only rarely encountered. This dimorphism has caused some confusion within the genus and several species have been described only later to be synonymized as the males of previously recognized taxa. The females usually form the base for the dichotomous keys used in identification. The male of *A. holmesi* has been unknown until this report, and so the description of the male is presented herein.

Male — slightly smaller than the female but similar in most features except as follows: 1) pleosome more massive; 2) antennae 1 and 2 (Figure 1A) with increased setation; 3) urosomite 2 (Figure 1C) more massive; 4) coxal plate 2 (Figure 1C) not quadrate posterolaterally; 5) increased pigmentation on head (Figure 1A); 6) uropod 2 (Figure 1C) with minute serrations; 7) uropod 3 more setose; 8) antenna 2 somewhat longer; and 9) gills of male "pleated," of female smooth.

As noted from the ecological notes presented in this paper, *A. holmesi* was collected from grass beds or areas

adjacent to grass beds. For this reason and for the earlier stated reason of several undescribed species in the northern and eastern Gulf of Mexico, we suggest that the records of Pearse (1912) be used with caution until a reexamination of that material is feasible.

Mills (1967, personal communication) has raised the question concerning the validity of the separation between *A. holmesi* and *A. verrilli*. Mills (1967) notes that to consider the two as conspecific "is unjustified" (p. 639) since an examination of extensive material has not revealed the presence of intermediate forms. A comparison of our material with the original work and the redescription by Barnard (1960) has shown our specimens to agree very well with published observations of *A. holmesi*. A critical comparison with specimens of *A. verrilli* from the type-locality has convinced us of the validity of the separation.

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AN UNUSUALLY SMALL EGG-CARRYING *CALLINECTES SAPIDUS* IN THE NORTHERN GULF OF MEXICO, WITH COMMENTS ON THE BARNACLE *LOXOTHYLACUS TEXANUS*

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ABSTRACT This communication reports the smallest verified egg-carrying specimen of *Callinectes sapidus*. With a carapace 20 mm long by 47 mm wide, the female measures considerably less than most other mature individuals, but about the same as an average-sized individual infected with an adult specimen of the rhizocephalan *Loxothylacus texanus*.

We report what we believe to be the smallest known egg-bearing specimen of *Callinectes sapidus* Rathbun. The crab's identification is based primarily on the two broad triangular frontal teeth on the carapace, orange-red coloration at the articulations, and orange fringes on chelae tipped with purple (Williams 1974; verified by Williams, personal communication). Using the specified dimensions described by Williams (1974), the specimen measured 20.0 mm long by 36.0 mm wide at the bases of lateral spines and 46.7 mm wide including the lateral spines (Figure 1). The crab, deposited in the Gulf Coast Research Laboratory Museum (GCRL 1121), came from 0.9 meters of 17-ppt water (29°C) on 14 June 1983, immediately south of Raccoon Point on the westernmost island of the Isle Dernières chain delimiting Caillou Bay, Louisiana. Its egg mass appeared brown because the orange-colored embryos had already developed large darkly pigmented eyes.

Initially, the berried crab occurred with three individuals parasitized by the rhizocephalan cirriped *Loxothylacus texanus* Boschma and was mistakenly considered to be infected. In fact, most small portunids with a semisubcircular-shaped abdomen shown to us by fishermen who thought they had mature females were infected by the rhizocephalan. The mature parasite has a protruding externa similar in appearance to a crab's egg mass. Mature uninfected female specimens of *C. sapidus* slightly larger than the one we report are known. Williams (1974) examined one 21 mm long by 55 mm wide, including lateral spines, and Fischler (1959) reported three 22 to 24 mm long by 52 to 55 mm wide from North Carolina where the parasite apparently did not exist.

Causes for dwarfing in *C. sapidus* are poorly understood. We know that the rhizocephalan *L. texanus*, which ranges from at least Panama (Boschma 1950) to Biscayne Bay, Florida (Overstreet 1983), stunts growth and feminizes



Figure 1. Egg-bearing *Callinectes sapidus* (GCRL 1121) next to a 17.9-mm-diameter U. S. ten cent coin.

males (e.g., Overstreet 1983). About one half of the rhizocephalan-infected crabs that we examined ranged between 40 and 55 mm wide (Figure 2), and the average width for infected ones in Louisiana collections was 58 mm (Adkins 1972). These parasitized crabs were smaller than mature females from the same locality (Figure 3). Other disease agents as well as genetic and environmental influences may also cause individuals to be abnormally small. For example, Tagatz (1968) reported that a much larger percentage of

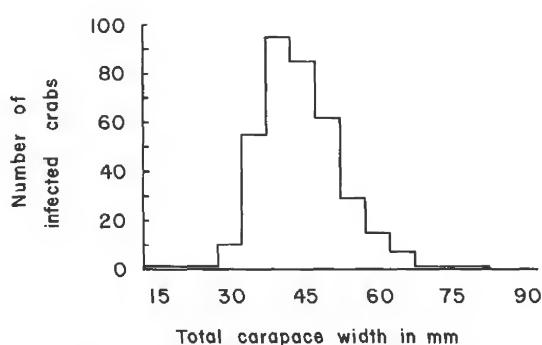


Figure 2. Carapace-widths (including lateral spines) of 364 individuals of *Callinectes sapidus* from Mississippi from October 1973 to September 1982 that had one or more externae of *Loxothylacus texanus* or a modified abdomen suggesting the rhizocephalan infection.

females matured at a small size in water ranging from 3- to 33-ppt salinity near the mouth of the St. Johns River in Florida compared with those in water usually less than 1 ppt in the same river south of Jacksonville.

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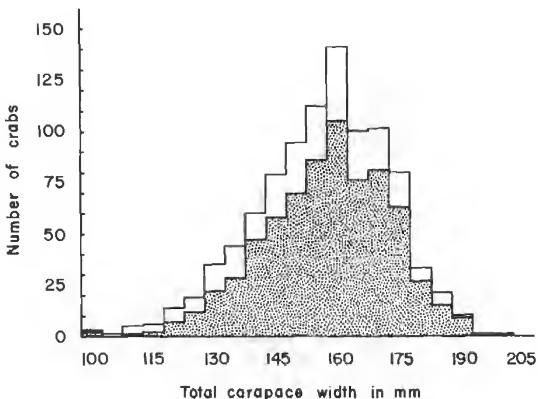


Figure 3. Carapace-widths (including lateral spines) of 960 mature females of *Callinectes sapidus* from Mississippi measured from October 1973 to September 1982 (white bars), overlayed by those females either carrying eggs or spawned at least once (dotted bars).

crab collected during the 1983 SEAMAP Project and Austin B. Williams, of the Systematics Laboratory, National Marine Fisheries Service, who verified the crab's identity and reviewed the manuscript. The work was conducted in cooperation with the U. S. Department of Commerce, NOAA, NMFS, under PL-88-309, Project No. 2-393-R.

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